2010

An Analysis of Anchitherine Equids Across the Eocene–Oligocene Boundary in the White River Group of the Western Great Plains

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AN ANALYSIS OF ANCHITHERINE EQUIDS ACROSS THE EOCENE–OLIGOCENE BOUNDARY IN THE WHITE RIVER GROUP OF THE WESTERN GREAT PLAINS

by

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A THESIS

Presented to the Faculty of

The Graduate College at the University of Nebraska

In Partial Fulfillment of Requirements

For the Degree of Master of Science

Major: Geosciences

Under the Supervision of Professors Ross Secord and Robert M. Hunt, Jr.

Lincoln, NE

April, 2010

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Anchitherine horses are a subfamily of equids that are abundantly represented in the late Eocene and early Oligocene of North America. This group has been heavily studied in the past, but important questions still remain. Some studies have focused on the Eocene-Oligocene boundary and have used these equids along with other taxa to study mammalian diet and climate change through this interval. I reexamine two anchitherine genera, *Mesohippus* and *Miohippus*, from stratigraphic sequences of the White River Group in western Nebraska and southwestern South Dakota. These sequences span the Chadronian (late Eocene), Orellan (early Oligocene), and Whitneyan (early Oligocene) North American land-mammal ages. The most recent revision of these genera was done by Prothero and Shubin (1989). I review the characters used for taxonomic identification. This includes characters such as the hypostyle, the articular facet on the third metatarsal, and dental dimensions. To avoid possible biases caused by combining specimens from different stratigraphic levels, specimens were separated by location and stratigraphic level. The length and width of cheek teeth, and tooth rows were measured on 488 specimens. First molar area serves as a proxy for body mass in horses and other mammals, and can be useful for distinguishing among species. Results indicate that the characters used by Prothero and Shubin were highly variable in anchitherine horses and are not useful for distinguishing between these genera. The development of the articular facet on the third metatarsal may be a function of body size

and therefore may be of no more utility than first molar area. Variability in first molar area suggests the presence of three species in the medial and late Chadronian, two species in the Orellan, and at least two species in the Whitneyan. Due to a lack of objective criteria separating *Mesohippus* from *Miohippus*, I recommend synonymy of these genera, making *Mesohippus* a junior subjective synonym.

DEDICATION

This thesis is dedicated to my wife, Julie, who has been there for me throughout my geology education at UNL, and to my parents, John and Elaine Masciale, who encouraged me to follow my dreams. I would also like to thank the rest of my family and friends who have encouraged me through graduate school. Their support and encouragement was a valuable aid.

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INTRODUCTION

Equids were one of the first groups used to illustrate an evolutionary sequence due to their abundance and general evolutionary trends in the fossil record. Early phylogenies conveyed equid evolution as a single lineage (Marsh 1879), while later phylogenies presented a branching phylogeny (Simpson 1951a; MacFadden 1992). The subfamily "*Anchitheriinae*" is one of three Equidae subfamilies, though MacFadden (1998) stated that this subfamily might be paraphyletic. Basal anchitherine equids have been heavily studied in the past, but there have been few recent studies focused on these horses. Some studies have focused on the Eocene-Oligocene boundary and have used these equids, along with other taxa, to provide information about the event. The genera *Mesohippus* and *Miohippus* are the basal members of the anchitherine horses, and are found in late Duchesnean–Arikareean deposits. These horses were first described by Leidy (1850, 1852), Marsh (1874, 1875), and Cope (1874, 1889), and several species were named. Osborn (1904) later named additional species. Among early authors examining these horses, Scott (1941) presented the most thorough description, and described the craniodental and postcranial anatomy of these genera.

Many early authors created a new species for every anatomical variation they observed. Stirton (1940) reported 20 species of *Mesohippus* and 18 species of *Miohippus*. Later authors recognized that not every anatomical difference justified naming a separate species. Simpson (1951b, 1961) recognized that species recognition based on a single type specimen was impractical, and argued that the most practical way to distinguish a species in the fossil record based on the biological species concept (Mayr, 1942) is to define species based on a population. Clark and Beerbower (1967) followed this model. Their study combined many of the previously recognized species of *Mesohippus* from the Chadron Formation of South Dakota into fewer species. Forstén (1970a, 1970b) further reduced the number of species of *Mesohippus*. Prothero and Shubin (1989)

FIGURE 1. Map showing location of fossil localities.

presented the latest taxonomy of Chadronian through Whitneyan horses. They set out to examine equids from a statistical viewpoint incorporating stratigraphic information. Yet they decided that this approach was not necessary because of trends they observed in their study. They based much of their taxonomy on anatomical characters. They recognized time intervals where four or five species of similar size coexisted with few anatomical differences between recognized species. Their explanation for this was that if the horses were to be stratigraphically useful, species of similar size could not be lumped together.

It is apparent that further study needs to be done to resolve the taxonomy of theses horses. MacFadden stated (1998), "Despite the work of Prothero and Shubin (1989) for the Orellan and Whitneyan forms, the specific taxonomy of all valid species of *Mesohippus* still needs to be done in a synthetic manner." I use body size and anatomical features of specimens from Nebraska and South Dakota localities (Fig. 1) to recognize species of anchitherine equids from the Chadronian and Orellan.

MATERIALS AND METHODS

The length and width of cheek teeth (P2–M3 and p2–m3) were measured in each specimen (individual measurements presented in Appendix A and B). When left and

right teeth were available, both were measured and then averaged. These measurements were used to compute the natural log of the area of M1, which is a proxy for body size (MacFadden, 1986). Gingerich et al. (1982) showed that the first molar is the least variable tooth in primates. M1 was chosen instead of m1 because lower teeth have few diagnostic features and upper teeth are more informative for species assignment in equids (MacFadden, 1986; Prothero and Shubin, 1989).

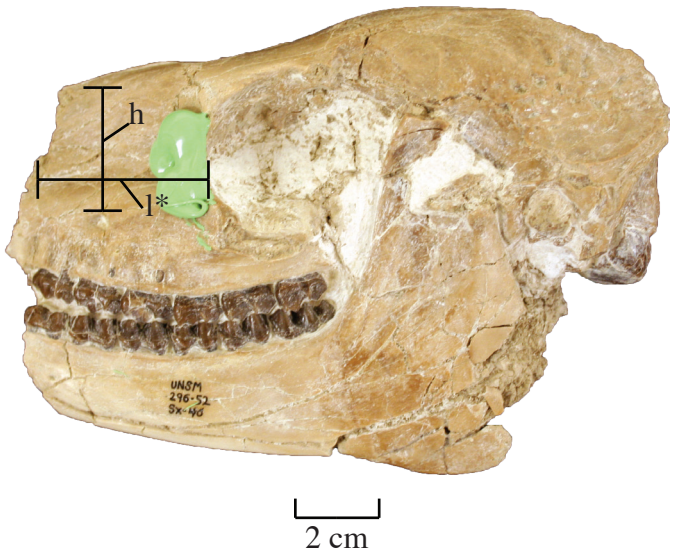

FIGURE 2. Skull of *Miohippus bairdii* (UNSM 131615), showing measured features of preorbital fossa. Silicone mold just anterior to the orbit was used to measure the depth. **Abbreviations**: **h**, height, **l**, length, *, length was not measured in this specimen as skull is not complete.

Specimens (from the University of Nebraska State Museum) with uncrushed facial regions were examined to measure the dimensions of the preorbital fossa. The length, height, and depth of the fossa were measured (Fig. 2). The height of the fossa was measured above the infraorbital foramen. The depth of the preorbital fossa was measured just anterior to the orbit, since it is the deepest part of the fossa (Prothero and Shubin, 1989). To measure the depth of the preorbital fossa, I created a mold of the fossa by injecting it with silicone (Fig. 2). The thickness was then measured.

Third metatarsals from the University of Nebraska State Museum were examined. The length and width of the region connected to the facet, the facet, and the angle of inclination were measured. The length and width of the region where the articular facet would be was also measured in specimens without an articular facet.

Statistical Analysis

In order to use size as a distinguishing characteristic for species identification, the difference in size between two species must be significant. One-way ANOVA tests using M1 length were conducted between identified species. Species from the same biozone within and between collecting localities were compared to establish if the difference in size was significant.

Species Classification

In order to taxonomically classify equids from this interval, I have used a population based approach. While specimens from the Whitneyan and Arikareean land-mammal ages were examined, my focus was on taxa from the Chadronian and Orellan land-mammal ages. Specimens were first separated by biozones. Specimens within a biozone were then tested for bimodality using M1 length. I examined variability using standard deviation, standard error, and coefficient of variation. I also looked for anatomical differences between specimens. When bimodality, large amounts of variability, significant differences in M1 length, or anatomical differences were present, I recognized the presence of more than one species.

I examined 221 specimens from the University of Nebraska State Museum in Lincoln, NE, 150 specimens from the Field Museum of Natural History in Chicago, IL, and 117 specimens from the South Dakota School of Mines and Technology Museum of Geology in Rapid City, SD. Only specimens that could be accurately placed stratigraphically were used in the analysis. Some workers studying this interval have

been critical of the stratigraphic data associated with specimens from the University of Nebraska State Museum, preferring specimens from areas in Wyoming such as Flagstaff Rim (Prothero and Emery, 1996a, 2004; Prothero and Whittlesey, 1998). While it is true that many White River Group specimens in the UNSM have little or no associated stratigraphic information, many equids have stratigraphic information that allows for accurate placement in a stratigraphic column. In some instances a stratigraphic range was indicated, e.g. 10–20 ft above the Upper Purple White. In these cases the average value of the range was used.

Institution Abbreviations

CM, Carnegie Museum of Natural History; FMNH, Field Museum of Natural History; MCZ, Harvard University Museum of Comparative Zoology; SDSM, South Dakota School of Mines and Technology Museum of Geology; UCMP, University of California Museum of Paleontology; UNSM, University of Nebraska State Museum; USNM, United States National Museum; YPM, Yale Peabody Museum of Natural History.

BACKGROUND

Lithostratigraphy

The White River is a formation in Wyoming and Colorado and a group in Nebraska and South Dakota. The White River Group is a group of lithologic formations, currently consisting of the Chamberlain Pass, Chadron, and Brule formations (LaGarry, 1998; Terry, 1998). Each formation has been divided into members regionally. White

River deposits are exposed best in Nebraska, South Dakota, and Wyoming. These deposits are Chadronian through Arikareean in age. Meek and Hayden (1857) first described the White River Group as a series of unnamed formations. Wortman (1893) and Hatcher (1893) divided the White River Group into the *Titanotherium* Beds, *Oreodon* Beds, Barren Clays, *Leptauchenia* Layer, and *Protoceras* Beds, recognizing important taxa found at different levels. Darton (1899; 1903) gave these lithologic units formal names, renaming the *Titanotherium* Beds the Chadron Formation and incorporating the remaining beds into the Brule Formation. The *Oreodon* Beds became the Orella Member of the Brule Formation in Nebraska (Schultz and Stout, 1955) and the Scenic Member of the Brule Formation in South Dakota (Bump, 1956). The *Leptauchenia* Layer and *Protoceras* Beds became the Whitney Member of the Brule Formation in Nebraska (Schultz and Stout, 1955) and the Poleslide Member of the Brule Formation in South Dakota (Bump, 1956).

The White River Group is unconformably underlain by Cretaceous Pierre Shale in Nebraska and South Dakota. Many authors have recognized that the top of the Pierre Shale is weathered and pedogenically altered. This weathered layer has been referred to as the Interior Phase (Toepelman, 1922), Interior Formation (Wanless, 1922), Interior Paleosol Complex (Schultz and Stout, 1955), Interior Zone (Clark et al., 1967a), and Interior Paleosol (Martin, 1987). Retallack (1983) divided this zone in South Dakota into two distinct paleosols. The lower paleosol was named the Yellow Mounds Paleosol Series and was determined to have developed directly on the Pierre Shale surface in the Paleogene (Evans and Terry, 1994). Evans and Terry (1994) attributed the exposure and pedogenic alteration of the Pierre Shale to a drop in relative base level at the end of the Cretaceous in response to early Laramide uplift. Retallack (1983) named the upper paleosol the Interior Paleosol Series and determined that it developed on an alluvial surface.

Clark noted that there were sandstones in the Interior Zone but was unsure

if they were fluvial (Clark, 1937) or lacustrine (Clark et al., 1967b) in origin. These sandstones and the Interior Paleosol Series of Retallack (1983) were later described as the Chamberlain Pass Formation and as the basal unit of the White River Group (Terry and Evans, 1994; Evans and Terry, 1994). Evans and Terry (1994) describe the Chamberlain Pass Formation as a series of fluvial sandstone channel deposits, alluvial mudstone overbank deposits, and paleosols. These fluvial and alluvial deposits are likely derived from Mesozoic and Paleozoic sedimentary rocks in the Black Hills region that were eroded during regional uplift (Evans and Terry, 1994). Evans and Terry (1994) noted that fossils are sparse in the Chamberlain Pass Formation, but that they seem to indicate early Chadronian time. In South Dakota fluvial erosion cut paleovalleys in the sandstone, mudstone, and the Yellow Mounds Paleosol, allowing the Interior Paleosol Series to form (Evans and Terry, 1994; Clark and Beerbower, 1967). Terry (1998) recognized a similar series of paleosols and sandstones in northwestern Nebraska. There are regional differences between the deposits of Nebraska and South Dakota, and so the terms Yellow Mounds Paleosol Equivalent, Chamberlain Pass Formation, and Interior Paleosol Equivalent were extended to Nebraska deposits (Terry, 1998).

The Chadron Formation in Nebraska was subdivided stratigraphically by Schultz and Stout (1955). The Chadron Formation is composed of sandstone channel deposits and overbank siltstone deposits with a distinct green color, with occasional lacustrine limestone deposits (Schulz and Stout, 1955; Clark and Beerbower, 1967; Evans and Welzenbach, 1998). The Chadron Formation contains a large amount of volcaniclastic material that was reworked by rivers (Swinehart et al., 1985). Schultz and Stout (1955) divided the Chadron Formation into informal lithologic units, in place of members, named A, B, and C (Fig. 3). The Chadron B was further subdivided into the B1, B2, B3, and B4 units. The Chadron B and Chadron C were divided by a series of prominent marker beds that consist of paleosols, volcanic ashes, gypsum, and limestones (Terry and LaGarry, 1998). These marker beds were referred to as the

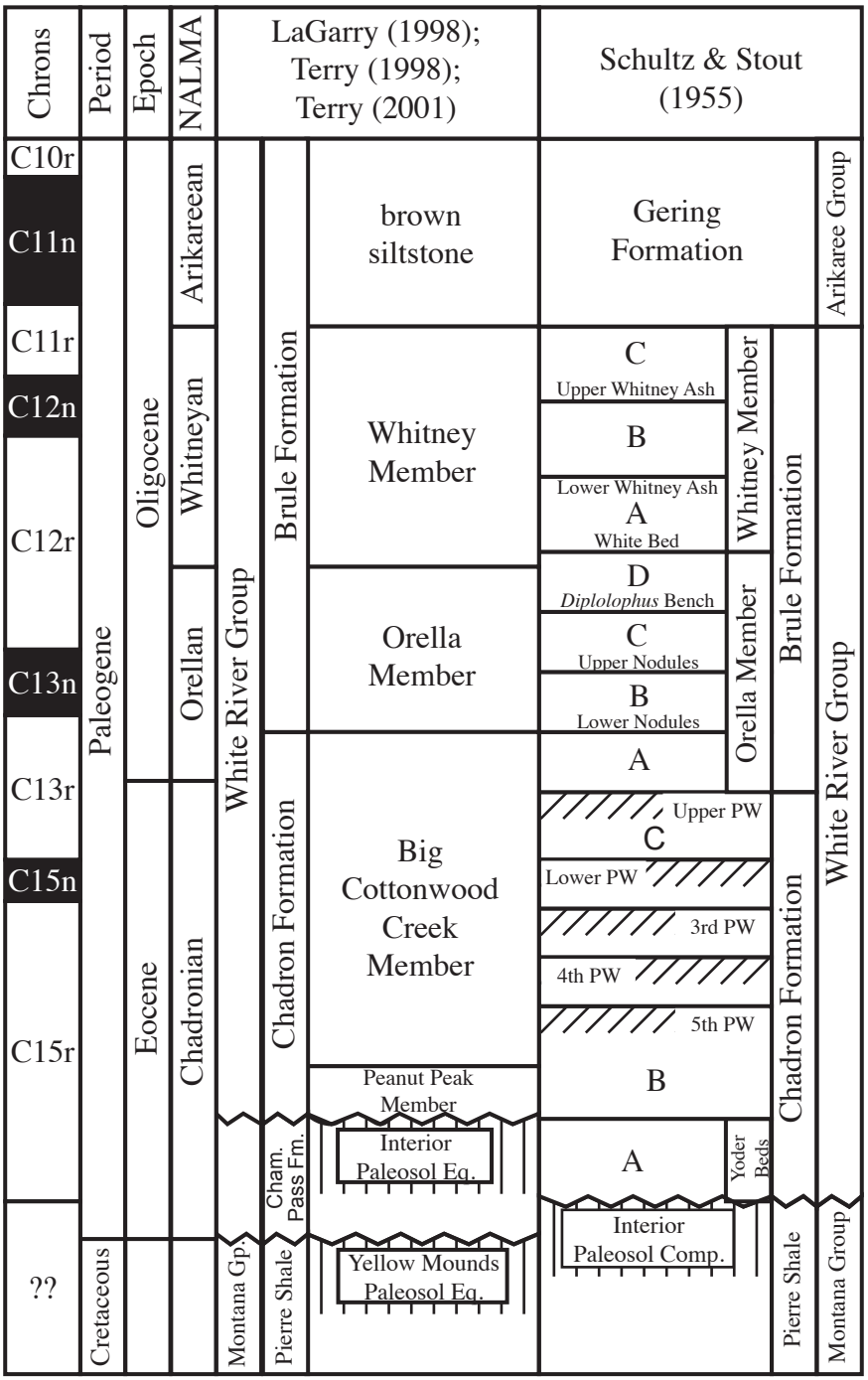

FIGURE 3. Current stratigraphic relationship of Toadstool Geologic Park (Nebraska). Stratigraphic units are not to scale. ?? indicates section not measured for magnetostratigraphy. **Abbreviations**: **C,** chron, **Cham.,** Chamberlain, **Comp.,** Complex, **Eq.,** Equivalent, **Fm.,** Formation, **Gp.,** Group, **n,** normal polarity, **r,** reverse polarity. Diagram modified from Terry (2001). Magnetostratigraphy: Swisher and Prothero (1990); Prothero and Swisher (1992); Prothero and Whittlesey (1998); Ogg and Smith (2004).

Purplish White Beds (PW) with the Fifth PW being the lowest stratigraphically. The Second PW and First PW are referred to as the Lower PW and Upper PW (UPW), respectively, and form the lower and upper boundaries of the Chadron C unit, respectively. The Chadron A or Yoder Beds of Schultz and Stout (1955) were reclassified as part of the Chamberlain Pass Formation (Terry, 1998; Terry and LaGarry, 1998). The lowest part of the Chadron B, essentially the B1 unit, was renamed the Peanut Peak Member, and the remainder of the Chadron B, Chadron C, and the Orella A unit from Schultz and Stout's (1955) Brule Formation were united to form the Big Cottonwood Creek Member (Terry and LaGarry, 1998).

The Brule Formation in Nebraska conformably overlies the Chadron Formation (LaGarry, 1998). Like the Chadron Formation, the Brule formation contains a large amount of fluvially reworked ash. Schultz and Stout (1955) divided the Brule Formation into the Orella and Whitney Members. They divided the Orella and Whitney members into informal stratigraphic zones referred to as A, B, C, and D and A, B, and C, respectively. The Orella A is made up of green to buff claystones. The Orella B begins with the lower nodules and consists of a similar lithology to the Orella A, except with numerous nodules, concretions, and sandstones intermixed with clay and siltstones. Another prominent nodular layer, the upper nodules, separates the Orella B from the Orella C. The Orella C is composed of laminated brown silt and clay with a thick channel complex that downcuts through the lower parts of the Orella Member in sections of Toadstool Park. The layer known as the Bench, now recognized as the serendipity ash (LaGarry, 1998), marks the boundary between the Orella C and the Orella D. The Orella D consists of brown to buff silt and claystones with several nodule layers.

The contact between the Orella and Whitney members was a layer known as the White Bed. The three divisions of the Whitney Member are composed of massive pink to buff siltsones and are separated by two ash layers, called the Lower Ash and the Upper Ash (Schultz and Stout, 1955). Terry and LaGarry (1998), LaGarry (1998), and

Swinehart et al. (1985) revised the Brule Formation in Nebraska based on lithology. Terry and LaGarry (1998) incorporated the Orella A of Schultz and Stout (1955) into the Big Cottonwood Creek Member of the Chadron Formation. LaGarry (1998) redefined the upper boundary of the Orella Member as 2.5–5.0 m below the White Bed. Swinehart et al. (1985) reclassified the lower Gering Formation overlying the Whitney Member (Schultz and Stout, 1955) as the brown siltstone member of the Brule Formation.

The Chadron Formation in South Dakota was stratigraphically subdivided by Clark (1937) and Clark and Beerbower (1967). The Chadron Formation is divided into three superposed members. From lowest to highest these are the Ahearn, Crazy Johnson, and Peanut Peak members (Fig. 4). The Chadron Formation of South Dakota, like that of Nebraska, contains a large amount of fluvially reworked volcaniclastics (Clark and Beerbower, 1967; Swinehart et al., 1985). The Ahearn Member was reportedly deposited at the base of a paleovalley and is composed of conglomerate, greenish sandstone, and siltstone (Clark and Beerbower, 1967). The Crazy Johnson Member is composed primarily of greenish to bluish bentonitic siltstones with occurrences of sandstone and conglomerate. It was reportedly deposited in the same paleovalley as the Ahearn Member (Clark and Beerbower, 1967). The upper member of the Chadron Formation is the Peanut Peak Member. The Peanut Peak Member reportedly overlies the paleovalley and is composed of tan to green siltstones, channel sandstones, and limestones (Clark and Beerbower, 1967). Analysis of clasts found in sandstones of the Chadron Formation by Clark and Beerbower (1967) and Evans and Terry (1994) reveals that the sandstones of the Chadron Formation are different from the sandstones of the Chamberlain Pass Formation. Evans and Terry (1998) determine that the sandstones of the Chamberlain Pass Formation were derived from the sedimentary Mesozoic and Paleozoic sedimentary rocks of the Black Hills. These sediments were shed during regional uplift of the Black Hills and the source material for the Chadron Formation was the newly exposed Precambrian igneous and metamorphic rocks of the Black Hills as the unroofing sequence

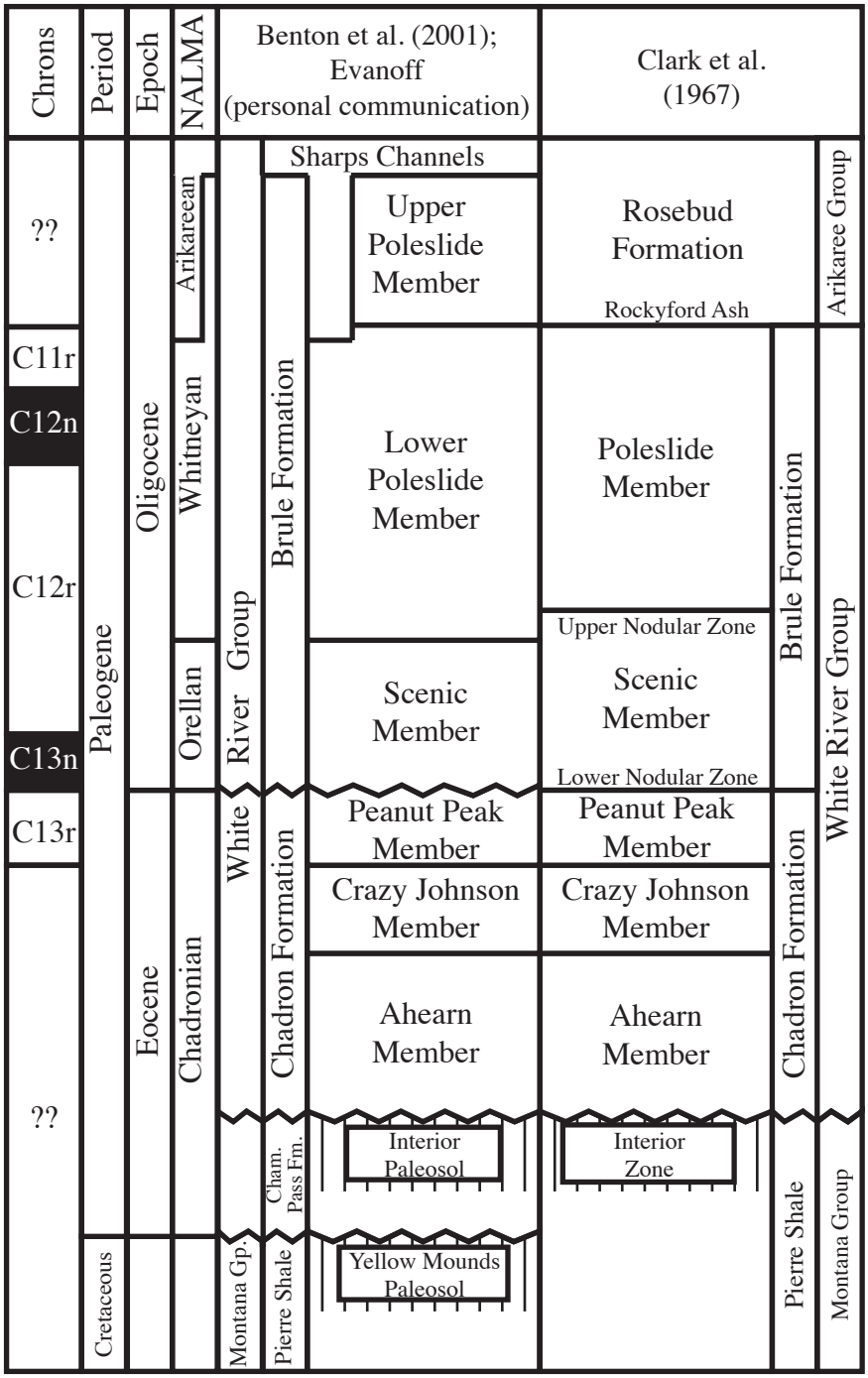

FIGURE 4. Current stratigraphic relationship of Badlands National Park (South Dakota). Stratigraphic units are not to scale. ?? indicates section not measured for magnetostratigraphy. **Abbreviations**: **C,** chron, **Cham.,** Chamberlain, **Fm.,** Formation, **Gp.,** Group, **n,** normal polarity, **r,** reverse polarity. Diagram modified from Terry (2001). Magnetostratigraphy: Swisher and Prothero (1990); Prothero and Swisher (1992); Prothero and Whittlesey (1998); Ogg and Smith (2004).

progressed (Evans and Terry, 1994).

Bump (1956), Clark (1967), Clark et al. (1967a), and Clark and Kietzke (1967) studied the Brule Formation in South Dakota. The Brule Formation in South Dakota does not conformably overlie the Chadron Formation and up to 1 million years may be missing in the South Dakota section (Prothero and Whittlesey, 1998). The Brule Formation is divided into the Scenic and Poleslide members. Bump (1956) recognized two prominent nodule layers, the "Lower Nodular Zone" and the "Upper Nodular Zone", as the lower and upper boundaries of the Scenic Member, respectively. The Scenic Member is made up of mudstone with sandstone sheets and paleosols. The Poleslide Member consists of siltstone with finer grained sandstone sheets than the Scenic Member. Benton et al. (2001) recognized that the lithology of the Poleslide Member first occurs 5.3 m below the Upper Nodular Zone and placed its base at this level. Evanoff (personal communication) divided the Poleslide Member into two units. The lower unit, the Lower Poleslide Member, combines the upper Scenic Member and the Poleslide Member of Bump (1956) and Clark et al. (1967a). The upper unit, the Upper Poleslide Member is the Rockyford Member (Rosebud Formation of Clark et al., 1967a) of the Sharps Formation, which consists of massive siltstones, carbonate nodules, and the Rockyford Ash (Benton et al., 2001; Evanoff, personal communication).

Tephrostratigraphy

The White River Group contains a large amount of volcaniclastic material. Volcaniclastics are present as ash layers and fluvially reworked ashes. The ash layers are important marker beds that can be radioisotopically dated, can be used to determine magnetic polarity, and can be used for stratigraphic correlation. The recognized ash beds in Nebraska are the following: the Lower Purplish White layer, the Upper Purplish White

layer (UPW), the Serendipity Ash, the Lower Whitney Ash and the Upper Whitney Ash, and the Nonpareil Ash from the Brown Siltstone Member (Fig. 3). The only recognized ash in South Dakota is the Rockyford Ash (Fig. 4), which has been renamed the Persistent White Layer (Evanoff, personal communication). Larson and Evanoff (1998) examined the tuffs of Nebraska. The Chadron and Orella tuffs are primarily rhyolitc to rhyodacitic, the Lower Whitney Ash is rhyodacitic, and the Upper Whitney Ash and Nonpareil Ash are dacitic. The tuffs of the Chadron Formation and the Whitney Member are coarser than the tuffs of the Orella Member. Larson and Evanoff (1998) proposed that the source for White River Group ashes was probably eastern Nevada and western Utah in the Great Basin. Few of the ashes in Nebraska and South Dakota have been radioisotopically dated. The Lower and Upper Whitney ashes and the Nonpareil Ash were dated by Swisher and Prothero (1990) using $^{40}Ar/^{39}Ar$ methods. However, Prothero and Emery (2004) thought these dates were inaccurate due to excess ^{40}Ar. The Lower Whitney Ash has been redated and corrected by 0.65% (according to Kuiper et al., 2008) and has an $^{40}Ar/^{39}Ar$ age of 31.47 ± 0.06 Ma (Deino, 1996, in personal communication in LaGarry, 1998). Unfortunately none of the other ashes in Nebraska or South Dakota have been dated. The UPW was correlated with Ash J of Flagstaff Rim in the Granite Mountains of Wyoming, the 3c tuff at Douglas, Wyoming, and the Persistent White Layer at Lusk, Wyoming using phenocryst assemblages. Obradovich et al. (1995) dated the Ash J and reported an age of 34.58 ± 0.11 Ma (corrected by 0.65% according to Kuiper et al., 2008). Sahy et al. (2010) are currently attempting to constrain the ages of the ashes in Nebraska.

Biostratigraphy

Figure 5 displays the correlation between the Nebraska and South Dakota sections. Wood et al. (1941) defined the Chadronian as the time when *Mesohippus* and

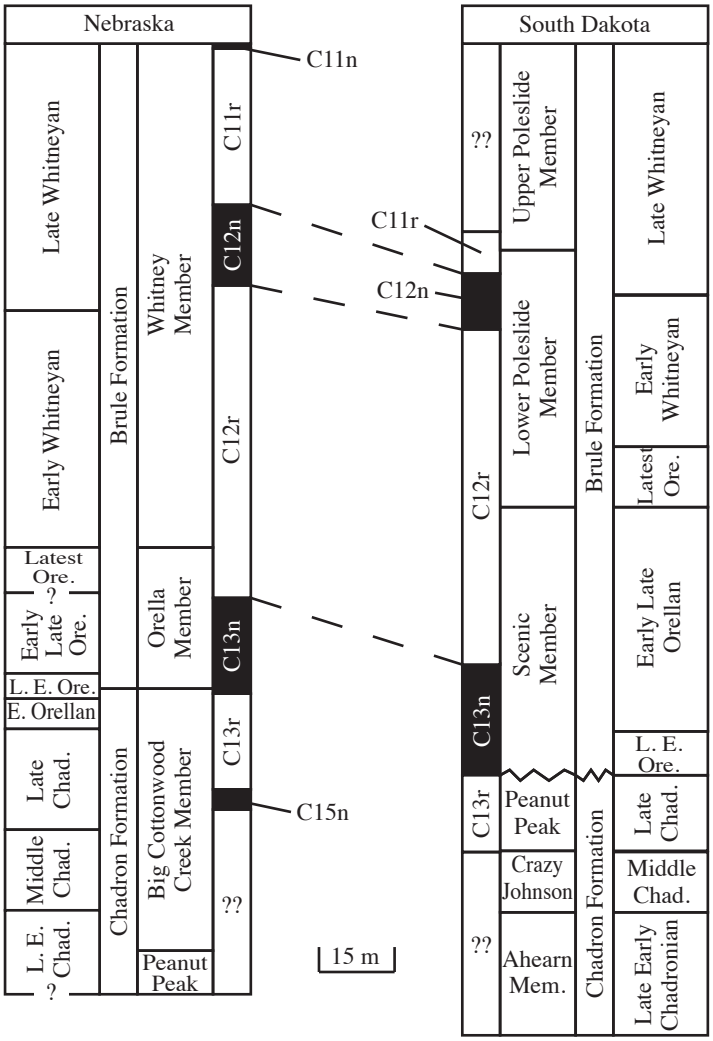

FIGURE 5. Correlation between Nebraska and South Dakota. **Abbreviations**: **Chad.**, Chadronian, **E.,** Earliest, **L.E.,** Late Early, **Mem.,** Member, **Ore.**, Orellan, **?**, Biozone boundary not defined, **??**, Magnetostratigraphy not reported. References: Swisher and Prothero (1990); Prothero and Swisher (1992); LaGarray (1998); Terry (1998); Prothero and Whittlesey (1998); Benton et al. (2001); Ogg and Smith (2004).

titanotheres coexisted. It was also based on the Chadron Formation, with the type locality near Chadron, Nebraska, and was applied to northwestern Nebraska and South Dakota. This definition combined lithologic units with biochronological units. Clark (1937, 1954) suggested that his divisions of the Chadron Formation could be used as time divisions of the Chadronian. Schultz and Falkenbach (1968) proposed oreodont faunal zones for Nebraska. Emery et al. (1987) recommended that the Chadronian be

defined in faunal terms. However, there were problems distinguishing the Duchesnean–Chadronian boundary at that time. Prothero and Emery (1996b) recommended sections from Trans-Peco, Texas, Flagstaff Rim, Wyoming, and Douglass, Wyoming, serve as the chronostratigraphic standards for the Chadronian. They suggested that the first appearances of *Bathygenys*, *Merycoidodon dunagani*, *Brachyrhynchocyon dodgei*, and *Archaeotherium* be used to recognize the beginning of the Chadronian, with *Bathygenys* as the defining taxon. Prothero and Emery (2004) formally defined the biozones of the Chadronian (Table 1). They divided the Chadronian into a series of interval zones, based on successive first occurences of species. Zanazzi et al. (2009) correlated the late

NALMA Subdivisions	Index Taxa	Biostratigraphic Type Section
Late Whitneyan (Wh–2)	*Merycoidon major*	30–103 m above old Scenic-Poleslide contact (Sheep MountainTable, SD)
Early Whitneyan (Wh–1)	*Leptauchenia major*	0–30 m above old Scenic-Poleslide contact (Sheep Mountain Table, SD)
Latest Orellan (Or–4)	*Merycoidon bullatus*	Upper Nodular Zone (Sheep Mountain Table, SD)
Early Late Orellan (Or–3)	*Miniochoerus gracilis*	27-50 m above PWL (Boner Ranch near Lusk, WY)
Late Early Orellan (Or-2)	*Miniochoerus affinis*	17-25 m above PWL (Boner Ranch near Lusk, WY)
Earliest Orellan (Or–1)	*Hypertragulus calcaratus*	7-17 m above tuff 5 (Douglas, WY)
Late Chadronian (Ch–4)	*Miniochoerus chadronensis*	25m below-7m above PWL (Boner Ranch near Lusk, WY)
Middle Chadronian (Ch–3)	*Leptomeryx mammifer*	15.24 m below Ash B-15.24 m above Ash G (Flagstaff Rim, WY)
Late Early Chadronian (Ch–2)	*Leptomeryx yoderi*	Just above base of section-15.24 m below Ash B (Flagstaff Rim, WY)
Earliest Chadronian (Ch–1)	*Bathygenys*	Reeves Bonebed section (Trans-Pecos, Texas)

TABLE 1. North American Land Mammal Age divisions. Zones are interval zones, with the first appearance of the index taxa signaling the start of a new zone. Biostratigraphy: Prothero and Whittlesey (1998); Prothero and Emery (2004).

early Chadronian at Toadstool Geologic Park in Nebraska as up to 34 m below the UPW. Zanazzi et al. (2009) correlated the middle Chadronian to between 34 m below the UPW to ~18 m below the UPW and the late Chadronian to between ~18 m below the UPW to ~2 m above the UPW at Toadstool Geologic Park in Nebraksa. Zanazzi et al. stated that it was possible that the end of the Chadronian might have been a diachronous event from state to state. Ogg and Smith (2004) presented an age of 33.9 Ma for the Eocene–Oligocene boundary, and Zanazzi et al. (2009) placed the Chadronian–Orellan boundary at this time.

Emery et al. (1987) reviewed the "oreodont faunal zones" of Schultz and Falkenbach (1968) for the Orellan, and found them to be inadequate zonations. Korth (1989) proposed a biostratigraphy of the Orellan based on mammals in the Orella Member of Nebraska. Prothero and Whittlesey (1998) found problems with Korth's (1989) biostratigraphy. Prothero and Whittlesey (1998) proposed that the first appearance of *Hypertragulus calcaratus*, with the first appearances of *Leptomeryx evansi* and *Palaeolagus intermedius* be used as biostratigraphic datum's to recognize the beginning of the Orellan, with *Hypertragulus calcaratus* as the defining taxon (Table 1). They divided the Orellan into a series of interval zones, based on successive first occurences of species. Zanazzi et al. (2009) correlated the earliest Orellan to between 2 to 8 m above the UPW and the late early Orellan to between 8 and 13 m above the UPW at Toadstool Geologic Park in Nebraska. The early late Orellan correlates to between 13 m above the UPW (Zanazzi et al., 2009) and near the top of Schultz and Stout's (1955) Orella C unit (Prothero and Wittlesey, 1998; Prothero and Emery, 2004). Prothero and Wittlesey (1998) and Prothero and Emery (2004) correlated the latest Orellan to the upper Orella C and Orella D, except the 2.5–5.0 m of the Orella D re-identified as part of the Whitney Member by LaGarry (1998), of Schultz and Stout (1955) at Toadstool Geologic Park in Nebraska.

Wood et al. (1941) defined the Whitneyan based on the Whitney Member of

the Brule Formation, with the type locality being Whitney, Nebraska. They correlated this to South Dakota and Wyoming, and included all uses of the terms *Protoceras* and *Leptauchenia* beds. Emery et al. (1987) pointed out that this definition was flawed, due to its use of a lithostratigraphic unit as a basis for a biostratigraphic unit. Prothero and Wittlesey (1998) and Prothero and Emery (2004) correlated the early Whitneyan to the Whitney A of Schultz and Stout (1955) in Nebraska. Prothero and Wittlesey (1998) and Prothero and Emery (2004) correlated the late Whitneyan to the Whitney B and C units of Schultz and Stout (1955). Tedford et at. (1996) defined the Whitneyan–Arikareean boundary by the first appearance of *Nanotragulus loomsi*, *Palaeolagus hypsodus*, *Palaeocastor nebrascensis*, *Leidymys blacki*, and *Mesoreodon minor*. This correlates to the Upper Poleslide Member near the "persistent white layer" in South Dakota and the "brown siltstone" member in Nebraska.

While Prothero and Whittlesey (1998), Prothero and Emery (2004), and Zanazzi et al. (2009) have updated the biostratigraphy of the White River Group, more work is needed. While Zanazzi et al. (2009) defined the biozones of Nebraska for the middle Chadronian–late early Orellan, the early late Orellan–late Orellan, late Orellan–early Whitneyan, and early Whitneyan–late Whitneyan boundaries in Nebraska need to be better defined. The biostratigraphy of South Dakota also needs revision. The mapping project undertaken by Benton et al. (2001) has produced fossils with accurate stratigraphic levels that will make the definition of biozones more precise for South Dakota.

Paleoclimate and Paleoenvironment

Several extinction events are now recognized near the Eocene-Oligocene (E–O) boundary. Extinctions and turnovers are recognized in calcareous nannoplankton

(Aubry, 1992), diatoms (Baldauf, 1992), mollusks (Hansen et al., 2004), and foraminifera (Keller et al., 1992; Thomas, 1992). The terrestrial deposits of Europe also show a large mammalian turnover. The event, known as the Grande Coupure, does not occur at the E–O boundary, but slightly after it (Prothero, 1994). Many of the archaic mammals present in the Headonian European land-mammal age are replaced by Asian taxa, such as rhinos, rodents, and artiodactyls (Prothero, 1994; Stehlin, 1909). Faunal turnover in North America is more modest. Land snails (Evanoff et al., 1992) and Brontotheriidae become extinct at or slightly above the E–O boundary.

The late Eocene–early Oligocene faunal changes correspond with climate change from 'greenhouse' to 'icehouse' conditions (Zachos et al., 2001). Zachos et al. reported a ~1‰ increase in $\delta^{18}O$ across the boundary, and attributed this to Antarctic glacier growth as lighter oxygen became trapped in ice. Glaciation in Antarctica is now thought to have lagged the E–O boundary (Coxall et al., 2005). This has led to a debate over whether there was a large temperature drop across the Eocene–Oligocene boundary. Some authors (Wolfe, 1978, 1992, 1994; Zanazzi et al., 2007; Zanazzi et al., 2009) have suggested large-scale (≥7 °C) cooling across the boundary in North America. Zanazzi et al. (2007) used fossil bone and enamel $\delta^{18}O$ values to estimate change in mean annual temperature across the E–O boundary. The $\delta^{18}O$ values for enamel showed no significant change, while $\delta^{18}O$ values for bone, which they presumed represented a reset, diagenetic signal, increased across the boundary by ~1.7 ‰. Combining these proxies, Zanazzi et al. (2009) calculated a temperature decrease of 7.1 ± 3.1 °C. Others have reported more protracted or smaller scale cooling in North America (Sheldon and Retallack, 2004; Sheldon, 2009). Stable conditions across the boundary have also been reported in Europe and South America (Grimes et al., 2003; Grimes et al., 2005; Kohn et al., 2004).

Sheldon (2009) criticized Zanazzi et al. (2007) for relying on diagenetic alteration of bone to calculate a temperature decrease. Zanazzi et al. (2007) argued that bone is altered within 20–50 kyr of burial, and that $\delta^{18}O$ bone values would reflect local water

composition and temperature. They then used $\delta^{18}O$ enamel values as a proxy for local meteoric water composition, allowing them to solve for temperature. However, Sheldon (2009) pointed out that the timing for diagenetic alteration is difficult to constrain. The diagenetically altered bone may not have been altered by surface water, but instead by ground water at a much later time. Sheldon (2009) also pointed out that paleosol studies have consistently concluded that there was a shift to more arid conditions in the early Oligocene and noted that this could drive the change in $\delta^{18}O$ values of bone. Therefore, Sheldon thought that some of the temperature drop reported by Zanazzi et al. (2007) could be attributed to a change to increasing aridity and concluded that a moderate temperature change was more likely. Other studies have also suggested increased aridity. Retallack (1992) and Terry (2001) suggested that there was increasing aridity from the late Eocene into the Oligocene, with semiarid conditions by 30 Ma (Sheldon and Retallack, 2004). Part of this aridity has been attributed to the development of a rain shadow in northwestern North America due to the emplacement of the Cascade Range (Sheldon and Retallack, 2004).

Clark and Beerbower (1967) and Clark and Kietzke (1967) hypothesized that the northern Great Plains were woodlands in the late Eocene, but gave way to woodlands, open plains, and swampy plains in the Oligocene, as aridity increased. Retallack (1983, 1992) and Terry (2001) interpreted the region as forested in the late Eocene, changing to a combination of wooded and open terrain in the Oligocene, based on root traces and soil structure. Strömberg (2004) analyzed phytoliths and found less evidence for open areas in the Oligocene. She concluded that the region was mostly forested in the late Eocene and early Oligocene, but that there were minor components of grassland (~5–7%) in the latter. She reported that at least one rock unit (the brown siltstone member) suggested a slightly higher percentage of grassland (~12%). These grasslands are assumed to be entirely or predominantly C3, as C4 grasslands did not become abundant until ~7 Ma (Cerling et al., 1997). Zanazzi and Kohn (2008) inferred the presence of forested and

open areas and niche partitioning among genera in the Orellan based on $\delta^{13}C$ enamel values. *Mesohippus* in the Oligocene exhibited a large range of values (~5‰), suggesting that equids may have been partitioning resources amongst themselves.

RESULTS

Statistical Analysis

Figures 6 and 7 show the distribution of M1 length. There is a bimodal distribution in the earliest Chadronian–earliest Orellan (Fig. 6). Figures 8, 9, and 10

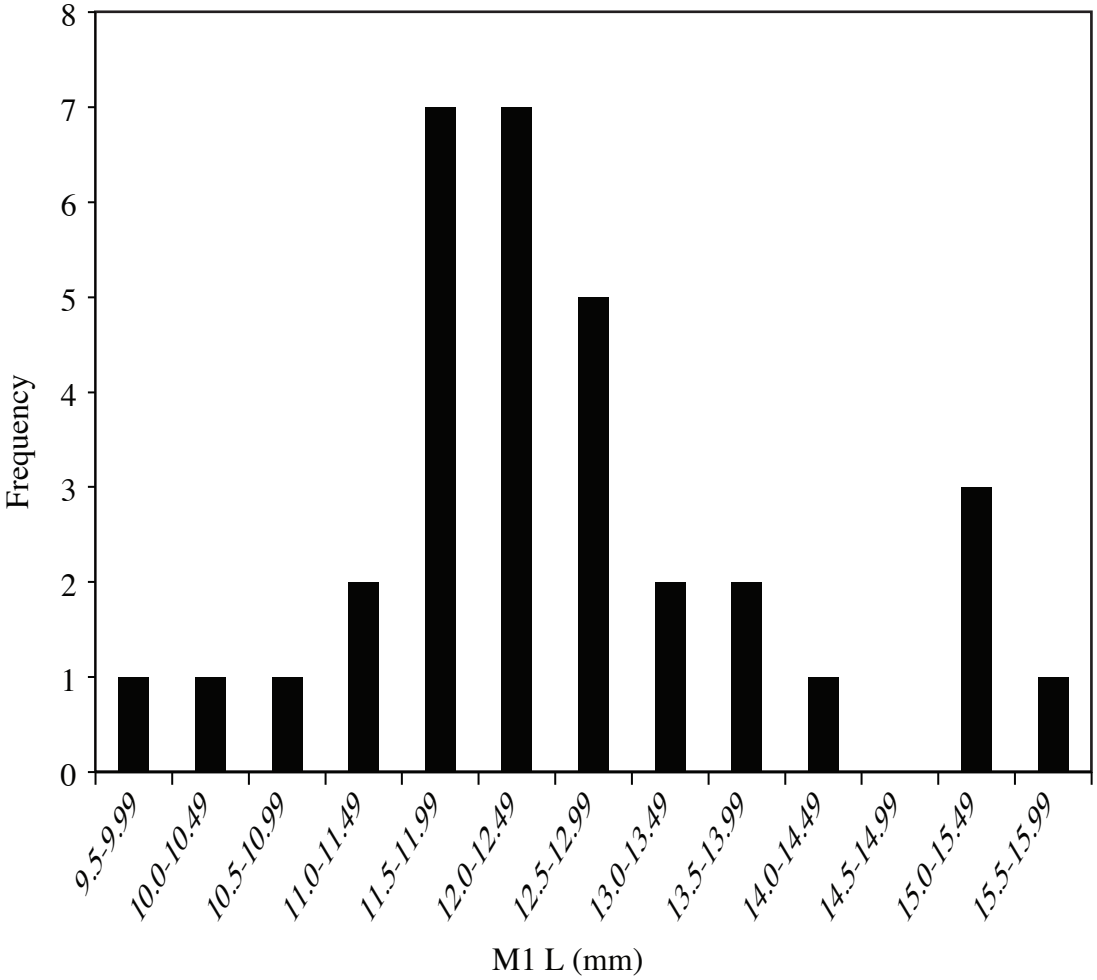

FIGURE 6. Distribution of M1 L (mm) of samples from the earliest Chadronian–earliest Orellan. The distribution is bimodal, suggesting that there are at least two body sizes present.

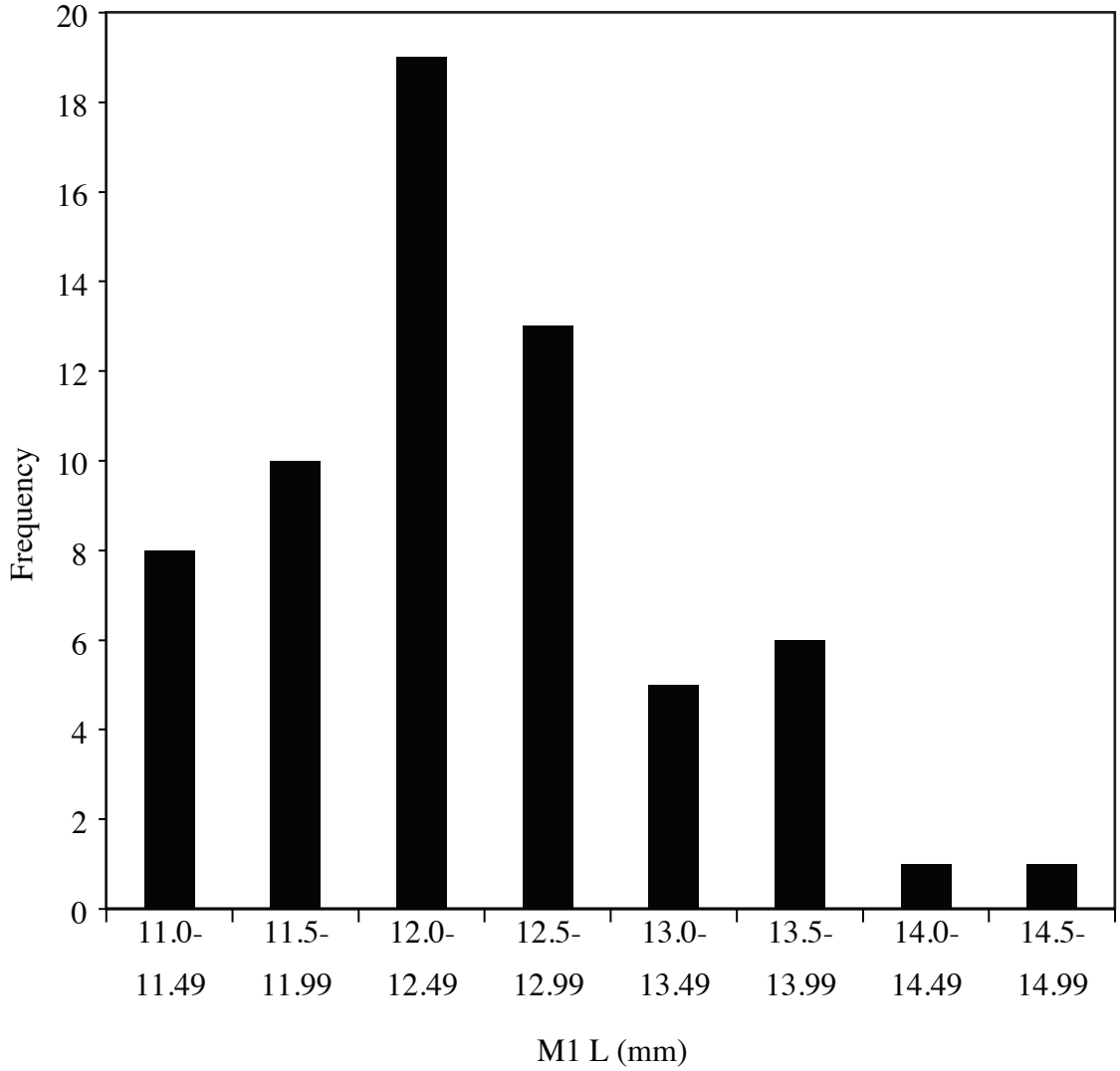

FIGURE 7. Distribution of M1 L (mm) of samples from the early late Orellan–latest Orellan. The distribution is skewed, suggesting that there are at least two body sizes present.

show natural log of M1 area, which is a proxy for body size (MacFadden, 1986). Table 2 displays the results of significance tests, one-way ANOVA. Table 3 shows the variability of M1 L in each biozone. There appear to be at least two species present in most of the Chadronian biozones based on body size. In the Chadronian three body sizes appear to be present based on the range of values. In the middle and late Chadronian there appears to be a 'small' and a 'large' horse, based on bimodality and the large difference in size values. In the earliest and late early Chadronian there is a third horse. This third horse is smaller than the 'small' horse from the middle and late Chadronian. Unfortunately no

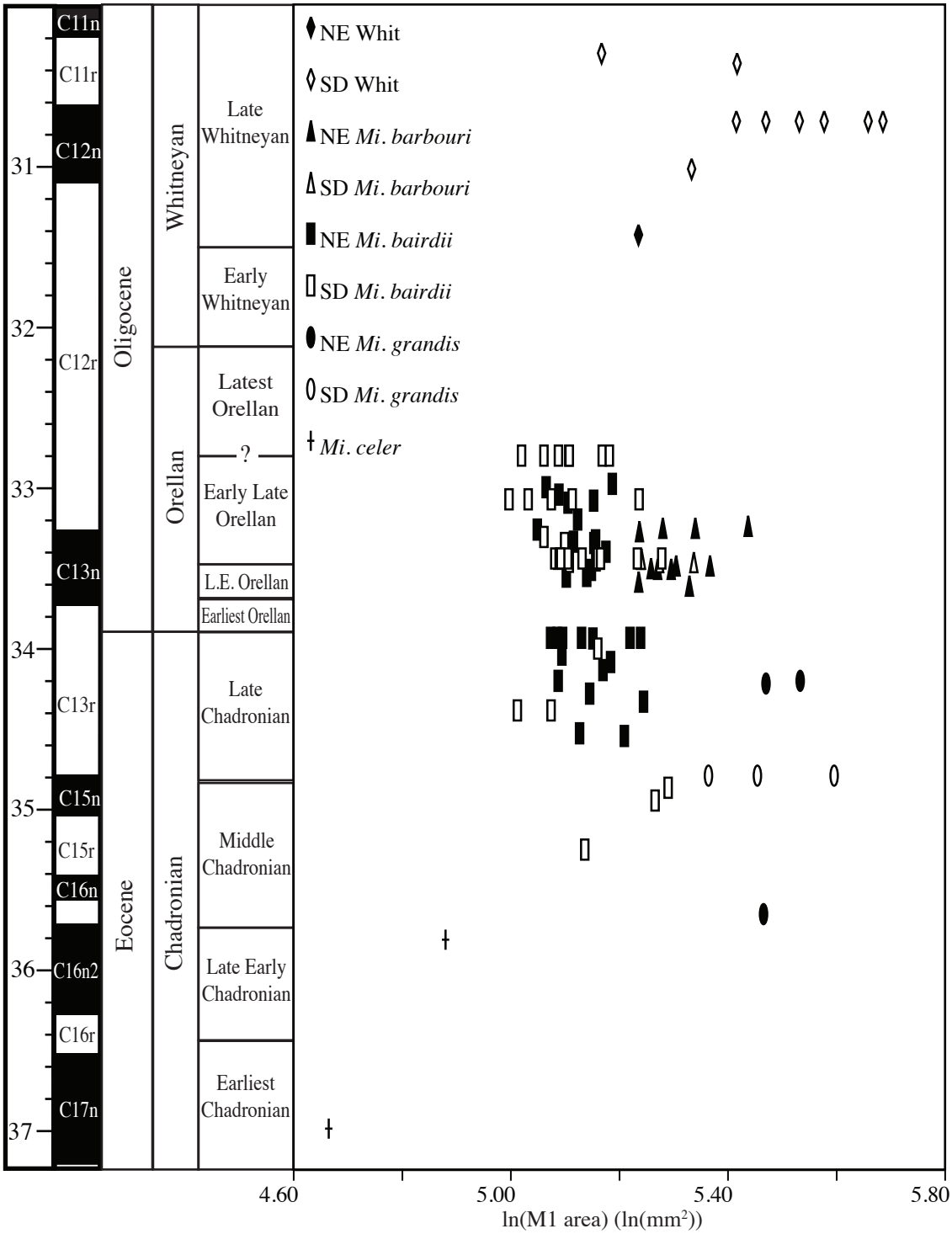

FIGURE 8. Natural log of M1 area showing differences in body size among equid samples. Magnetostratigraphy: Swisher and Prothero (1990); Prothero and Swisher (1992); Ogg and Smith (2004). Biostratigraphy: Prothero and Whittlesey (1998); Prothero and Emery (2004).

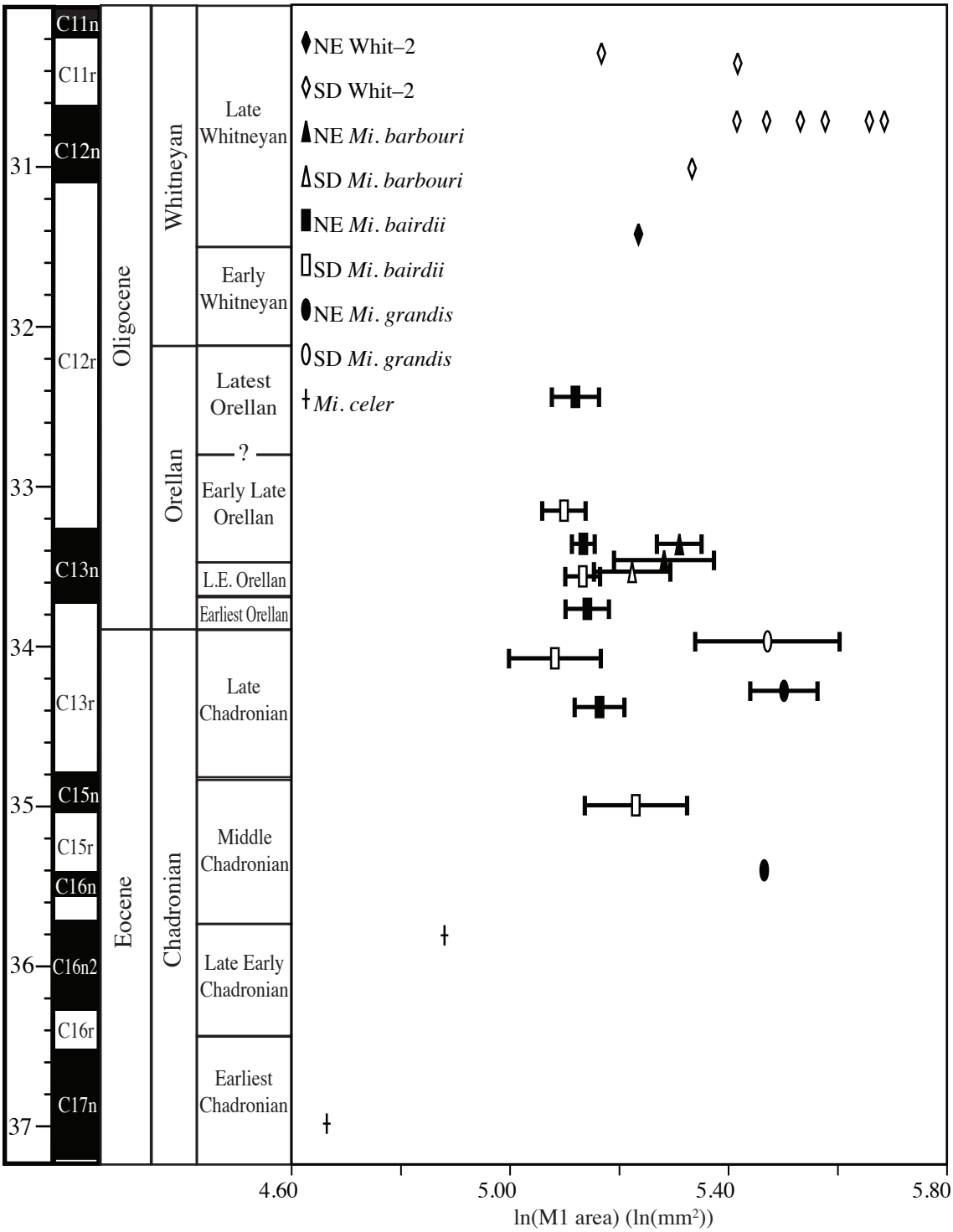

FIGURE 9. Natural log of M1 area showing differences in body size among equid samples. Symbols are mean values and error bars show 95% confidence (±1.96 SE). Standard error is the standard deviation of the error in the sample mean relative to the true mean. Symbols without error bars represent species with one sample per biozone. Magnetostratigraphy: Swisher and Prothero (1990); Prothero and Swisher (1992); Ogg and Smith (2004). Biostratigraphy: Prothero and Whittlesey (1998); Prothero and Emery (2004).

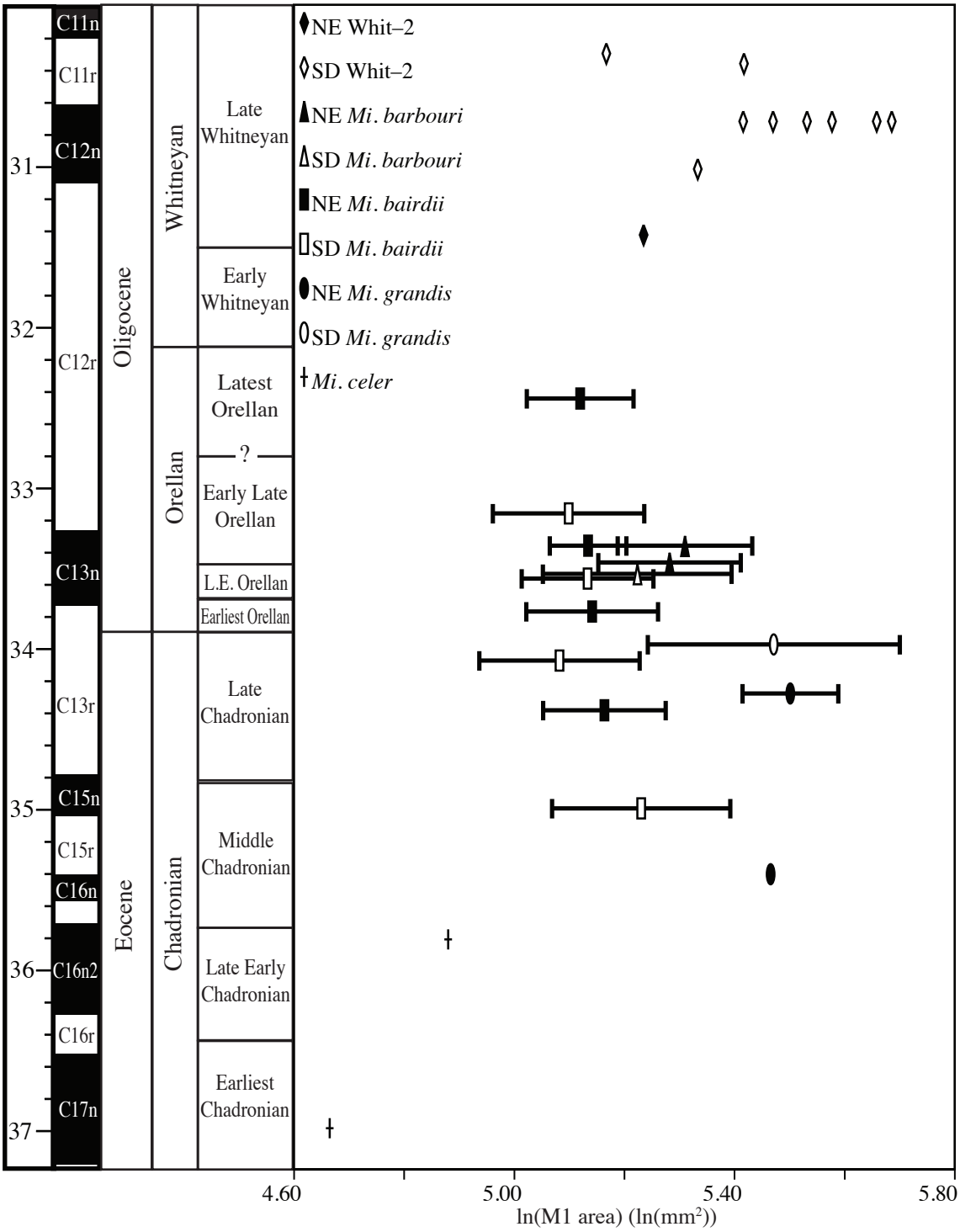

FIGURE 10. Natural log of M1 area showing differences in body size among equid samples. Symbols are mean values and error bars show 95% confidence (±1.96 SD). Standard deviation is the amount of variation there is from the mean of a sample. Symbols without error bars represent species with one sample per biozone. Magnetostratigraphy: Swisher and Prothero (1990); Prothero and Swisher (1992); Ogg and Smith (2004). Biostratigraphy: Prothero and Whittlesey (1998); Prothero and Emery (2004).

A. Nebraska	1	2	3	4	5	6	7	8	9	10
1. *M. bairdii* (Or)	1.000									
2. *M. barbouri* (Or)	**2.4E-11**	1.000								
3. *M. bairdii* (Or–4)	0.976	**7.8E-05**	1.000							
4. *M. bairdii* (Or–3)	0.629	**3.0E-08**	0.755	1.000						
5. *M. barbouri* (Or–3)	**6.1E-10**	0.902	**3.3E-04**	**2.4E-07**	1.000					
6. *M. barbouri* (Or–2)	**1.7E-05**	0.796	**0.009**	**2.3E-05**	0.753	1.000				
7. *M. bairdii* (Or–1)	0.671	**4.5E-07**	0.796	0.453	**3.8E-06**	**0.001**	1.000			
8. *M. grandis* (Ch)	**4.0E-11**	**0.002**	**4.3E-04**	**1.9E-08**	**0.006**	**0.031**	**2.8E-06**	1.000		
9. *M. bairdii* (Ch–4)	0.124	**2.7E-04**	0.368	0.228	**8.7E-04**	**0.022**	0.173	**2.6E-04**	1.000	
10. *M. grandis* (Ch–4)	**8.1E-09**	**0.011**	**0.003**	**5.4E-07**	**0.026**	0.094	**4.5E-05**	0.905	**0.002**	1.000

B. South Dakota	1	2	3	4	5	6	7	8
1. *M. bairdii* (Or)	1.000							
2. *M. bairdii* (Or–3)	0.772	1.000						
3. *M. bairdii* (Or–2)	0.790	0.634	1.000					
4. *M. barbouri* (Or–2)	**2.6E-04**	**0.003**	**4.6E-04**	1.000				
5. *M. bairdii* (Ch)	0.131	0.215	0.208	0.259	1.000			
6. *M. bairdii* (Ch–4)	0.669	0.839	0.553	**0.023**	0.396	1.000		
7. *M. grandis* (Ch–4)	**3.6E-09**	**1.7E-05**	**1.7E-07**	**0.004**	**0.009**	**0.010**	1.000	
8. *M. bairdii* (Ch–3)	**0.007**	**0.034**	**0.011**	0.929	0.432	0.167	0.075	1.000

C. Between States	1	2	3	4	5	6	7	8
1. *M. bairdii* (NE–Or)	1.000							
2. *M. bairdii* (SD–Or)	0.722	1.000						
3. *M. barbouri* (NE–Or)	**2.4E-11**	**1.1E-10**	1.000					
4. *M. barbouri* (SD–Or)	**1.5E-04**	**4.7E-05**	**0.024**	1.000				
5. *M. bairdii* (NE–Ch)	0.124	0.107	**2.7E-04**	0.087	1.000			
6. *M. bairdii* (SD–Ch)	0.148	0.131	**0.004**	0.259	0.910	1.000		
7. *M. grandis* (NE–Ch)	**4.0E-11**	**3.5E-10**	**0.002**	**8.7E-04**	**2.6E-04**	**0.004**	1.000	
8. *M. grandis* (SD–Ch)	**5.9E-10**	**3.6E-09**	**0.008**	**0.004**	**9.1E-04**	**0.009**	0.791	1.000

Wh	Whitneyan
Wh–2	*Merycoidodon major* Zone (Late Whitneyan)
Wh–1	*Leptauchenia major* Zone (Early Whitneyan)
Or	Orellan
NE–Or	Nebraska Orellan
SD–Or	South Dakota Orellan
Or–4	*Meycoidodon bullatus* Zone (Latest Orellan)
Or–3	*Miniochoerus gracilis* Zone (Early Late Orellan)
Or–2	*Miniochoerus affinis* Zone (Late Early Orellan)
Or–1	*Hypertragulus calcaratus* Zone (Earliest Orellan)
Ch	Chadronian
NE–Ch	Nebraska Chadronian
SD–Ch	South Dakota Chadronian
Ch–4	*Miniochoerus chadronensis* Zone (Late Chadronian)
Ch–3	*Leptomeryx mammifer* Zone (Middle Chadronian)
Ch–2	*Leptomeryx yoderi* Zone (Late Early Chadronian)

TABLE 2. Matrices of pairwise probabilities of mean differences in natural log of M1 area. Comparisons were made between species in Nebraska (A), South Dakota (B), and between the states (C). Values in bold indicate significance ($p < 0.05$) using one-way ANOVA tests.

specimens of the smallest horse were examined that come from the same biozone as the other two Chadronian horses reported here.

In the Orellan there appears to be at least two body sizes. The difference in size between species in the Orealln is not as great as the difference in size between the species in the middle and late Chadronian. The Orellan species seem to overlap in size (Fig. 9). However, there are anatomical differences, discussed in the Systematic Paleontology section, that suggest that these horses are separate species. Only a small sample of Whitneyan material was available for study, and these specimens have not been placed into species for this study. There appear to be at least two sizes present in the Whitneyan.

Biozone	n	SD	SE	V
NE Or–4	5	0.54	0.24	4.49
NE Or–3	21	0.86	0.19	6.75
SD Or–3	12	0.62	0.18	5.14
NE Or–2	3	0.47	0.27	3.52
SD Or–2	22	0.60	0.13	4.86
NE Or–1	12	0.58	0.17	4.86
NE Ch–4	9	1.25	0.42	9.64
SD Ch–4	6	1.73	0.71	13.00
SD Ch–3	3	0.95	0.55	7.29

TABLE 3. Variability of M1 L in each biozone. Biozone abbreviations same as Table 2. **Abbreviations**: **n**, number of individuals, **SD**, standard deviation, **SE**, standard error, **V**, coefficent of variation.

Significance tests, one-way ANOVA, were used to test the difference in M1 length of contemporaneous species in a given biozone. Identification of species is discussed in the Systematic Paleontology section. Significant differences ($p < 0.05$) were found between *Miohippus bairdii* and *Miohippus grandis* M1 length from the late Chadronian in Nebraska and South Dakota. The difference between these two species for the middle Chadronian and late Chadronian combined are significant ($p < 0.05$) in South Dakota and Nebraska (Table 2). Comparison of *Miohippus bairdii* samples in Nebraska and South Dakota reveal that there are not significant ($p > 0.05$) differences between these samples in the middle–late Chadronian. This is also true for interstate comparisons of *Miohippus grandis* in the Chadronian.

Miohippus bairdii and *Miohippus barbouri* begin their coexistence in the late early Orellan. Comparison of theses species from the late early Orellan of South Dakota

indicates that there is a significant difference between them. There is also a significant difference in size between *Miohippus bairdii* and *Miohippus barbouri* from the early late Orellan of Nebraska. Interstate comparison reveals that there is not a significant difference between the two populations of *Miohippus bairdii* in the Orellan. There is a significant difference, however, between the interstate samples of *Miohippus barbouri* in the Orellan. The specimens of *M. barbouri* from South Dakota are all smaller individuals (M1 length < 13.5 mm), although the sample from South Dakota is fairly small (n=6). Over half of the specimens from Nebraska are larger individuals. I suspect that the difference between the populations would not be significant with a larger sample size from South Dakota.

SYSTEMATIC PALEONTOLOGY

Order PERISSODACTYLA Owen, 1848

Family EQUIDAE Gray, 1821

Genus *MIOHIPPUS* Marsh, 1874

PALAEOTHERIUM Leidy, 1850 (in part)

ANCHITHERIUM Leidy, 1852 (in part)

MESOHIPPUS Marsh, 1875

PEDIOHIPPUS Schlaikjer, 1935

Type species—*Miohippus annectens* Marsh, 1874

Revised Description—Small to medium sized equids, typically ranging ~35–75 kg. P2/p2 are molariform. Metacarpal 5 is reduced or in most cases absent. Hypostyle present in most species.

Included species—*Miohippus acutidens, M. anceps, M. annectens*, *M. assiniboiensis*, *M. bairdii*, *M. barbouri*, *M. celer*, *M. condoni*, *M. equiceps*, *M. gemmarosae*, *M.gidleyi*, *M. grandis*, *M.* intermedius, *M. obliquidens*, *M. primus*, and *M. quartus*.

Biostratigraphic Occurrences—Late Duchesnean through early late Arikareean.

Revised Diagnosis—Longer face than *Epihippus, Orohippus, Haplohippus,* or *Hyracotherium*.

Discussion—Specimens later referred to *Mesohippus* were identified by Leidy in 1850 as *Palaeotherium*, and 1852 as *Anchitherium*. *Miohippus* was described by Marsh in 1874. The type of *Miohippus* is from the early Arikareean of the John Day Fossil Beds in Oregon. Marsh renamed Leidy's 1852 *Anchitherium* from the White River Group *Mesohippus* in 1875. The type of *Mesohippus* is from the late early Orellan of the badlands in South Dakota.

The distinction between *Miohippus* and *Mesohippus* has remained a point of contention for some time (Osborn, 1918; Prothero and Shubin, 1989; MacFadden, 1998. Osborn (1918) separated *Mesohippus* and *Miohippus* primarily by a stratigraphic boundary. Osborn also tried to find morphological differences between the genera, but most of these are not now considered valid character differences (Prothero and Shubin, 1989). Scott (1941) distinguished *Miohippus* from *Mesohippus* using size and the articulation between the third metatarsal and the cuboid. Prothero and Shubin (1989) used these two characters and the relative size of the facial fossa (preorebital fossa of MacFadden, 1992), to distinguish between these two genera. They also challenged the idea that *Miohippus* evolved from *Mesohippus* as part of a gradual evolutionary lineage, and presented a model of punctuated equilibrium. MacFadden (1998), on the difference between *Mesohippus* and *Miohippus*, stated "Although Prothero and Shubin (1989) have suggested that several diagnostic characters define *Mesohippus*, as Stirton (1940) suggested, these two genera are indeed difficult to separate. Stirton (1940) lists eighteen named species of *Miohippus;* however, like *Mesohippus*, a complete revision of all Oligocene and Miocene valid species (including those dealt with in Prothero and Shubin, 1989) referable to this genus is still needed."

The main trait previously used to distinguish *Mesohippus* and *Miohippus* is size.

Miohippus is recognized as the larger horse (see data in Prothero and Shubin, 1989). The later forms of *Miohippus* can be considerably larger than *Mesohippus*, but the recognized species of *Miohippus* that coexist with *Mesohippus* sometimes overlap in size (Prothero and Shubin, 1989). Body size should not be considered as a distinguishing character for generic recognition because the two genera overlap in size while coexisting.

The second recognized character is the articulation between the third metatarsal and the cuboid bones of the hind foot. Prothero and Shubin (1989) and Scott (1941) argued that in *Mesohippus* the metatarsal does not articulate with the cuboid, but it does in *Miohippus*. This articulation can be recognized by an articular facet on the third metatarsal (Fig. 11). Forsten (1974) stated that some facets on these third metatarsals may be weakly developed instead of undeveloped, and the developed facets vary in size from specimen to specimen. In examining the third metatarsal I discovered that there are three conditions instead of two. The developed articular facet articulates with the cuboid. The articular facet is oriented at ~39°. The second type of facet is partially developed. The surface area of the partially developed facet is smaller than that of the developed facet. The mean angle of orientation for the partially developed facet is 50.5° (see data in the Appendix D, Table D1). UNSM 131693 has articulated metatarsals with a partially developed articular facet contacting the cuboid (Fig. 12). I identified this specimen as *Miohippus bairdii*, based on the craniodental

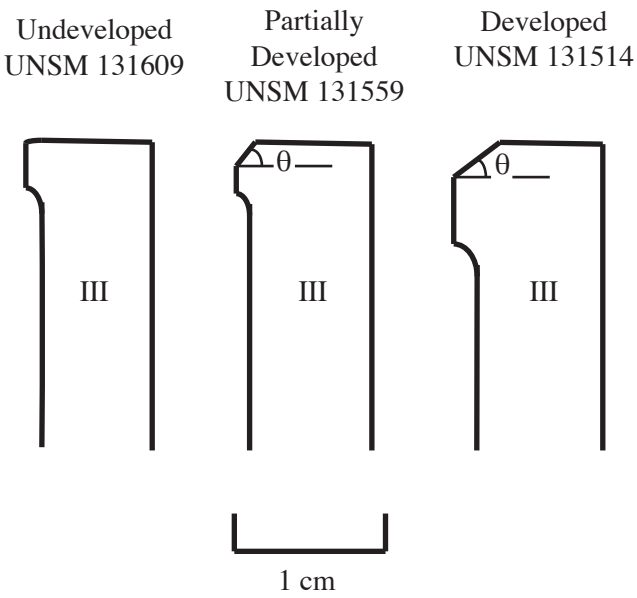

FIGURE 11. Conditions of the articular facet of third metatarsals found in *Miohippus*. θ is the angle of inclination.

material that I examined. The third condition, the undeveloped facet, suggests no articulation between the cuboid and the third metatarsal. The surface where the facet would be is vertical (~90°).

FIGURE 12. Partially developed third metatarsal of *Miohippus bairdii* (UNSM 131693). Arrow points to contact between metatarsal III and cuboid bone.

In equids weight is principally transferred through the navicular and ectocuneiform bones of the ankle to the third metatarsal (Hussain, 1975). "Transmission of weight from the cuboid to metatarsals III and IV depends on the facets for articulation with the navicular and also on the degree of development of the facet for metatarsal III" (Hussain, 1975). Thus the consequence of the development of this facet is the distribution of more weight onto the third metatarsal and removal of weight from the fourth metatarsal. This suggests that the development of this facet may be associated with an increase in body weight. In younger genera this accompanies the reduction of lateral digits. In *Mesohippus* and *Miohippus* the second and fourth metatarsals do not reduce in size and in these horses they help to support the animal's weight. The

existence of fully developed, partially developed, and undeveloped articular facets suggests that both *Mesohippus* and *Miohippus* have reached a weight threshold and have begun to redistribute their weight. The lower angle seen in the developed articular facet suggests more weight transfer to the third metatarsal than would be seen in partially developed articular facets. The developed articular facet is seen in all younger genera. Younger horse genera, with the exception of *Archaeohippus*, are of similar size or larger than *Miohippus*. The variation in these facets then is to be expected as weight-bearing increases over time in *Mesohippus-Miohippus* species. Thus, because development of the articular facet should vary as different lineages increase in body size, it should be used with caution in systematic analysis. One specimen in the Nebraska State Museum, UNSM 131799, has two preserved third metatarsals, one undeveloped and one partially developed. This provides further evidence that the presence of the articular facet on the third metatarsal should not be used a diagnostic character to separate these genera.

A. Miohippus	n	Min.	Max.	Mean	SE	SD
P. O. F. L	3	58.0	70.0	62.5	3.74	6.48
P. O. F. H	3	23.1	31.0	27.1	2.27	3.93
P. O. F. D	3	4.85	5.85	5.39	0.29	0.50
P. O. F. L/size	3	10.5	13.3	11.5	0.90	1.56
P. O. F. H/size	3	4.16	5.60	4.97	0.43	0.74
P. O. F. D/size	3	0.92	1.05	0.99	0.04	0.06
B. *Mesohippus*	n	Min.	Max.	Mean	SE	SD
P. O. F. L	9	45.0	63.3	52.5	2.09	6.26
P. O. F. H	10	17.3	24.8	20.1	0.75	2.38
P. O. F. D	9	3.19	5.48	4.42	0.24	0.73
P. O. F. L/size	5	8.73	12.4	10.4	1.55	0.69
P. O. F. H/size	6	3.37	4.78	3.92	0.51	0.21
P. O. F. D/size	5	0.62	1.08	0.87	0.19	0.08

TABLE 4. Descriptive statistics for the preorbital fossa between specimens classically identified as *Miohippus* and *Mesohippus*. Natural log of M1 area was used as a proxy for body size. **Abbreviations**: **D**, depth, **H**, height, **L**, length, **P. O. F.,** preorbital fossa. Other abbreviations same as TABLE 3.

The preorbital fossa has been used as a character to distinguish between *Mesohippus* and *Miohippus*. Comparisons of the preorbital fossa between the genera has been fairly subjective, with workers (Osborn, 1918; Prothero and Shubin, 1989) stating that *Miohippus* has a longer and/or deeper fossa than that of *Mesohippus* without providing data to back up these statements. The fossa can be difficult to measure because an uncrushed skull with

an intact facial region is needed. The length of the fossa is difficult to quantify because in some specimens it begins just above P2 and in others, just posterior to the canines (see Osborn, 1918 for illustrations). The fossa supposedly housed a greatly expanded nasal diverticulum, a feature that may have been used in vocalization (Gregory, 1920; MacFadden, 1984).

Table 4 displays descriptive statistics of the preorbital fossa. Table 5 displays significance test results, one-way ANOVA. While the preorbital fossa of *Miohippus* is longer and deeper than that of *Mesohippus*, the ratios of lenght/size and depth/size are not significantly different ($p < 0.05$). The difference in ratios between *Miohippus* and *Mesohippus* should be significant if the difference in the size of the preorbital fossa is not due to an increase in body size. Two of the *Miohippus* sampled are from the Whitneyan and the Arikareean. The specimens of *Miohippus* examined were all larger than the specimens of *Mesohippus* sampled (see data in the Appendix D). The deeper and longer preorbital fossa of *Miohippus* is due to its larger skull. The increase in size of the preorbital fossa is more closely related to the change in body size, rather than a change in dimensions. This is seen in the difference between *Miohippus intermedius* and *Miohippus gidleyi* (Prothero and Shubin, 1989). *Miohippus gidleyi* is larger than *Miohippus intermedius*, and the fossa of *Miohippus gidleyi* is broader and deeper than that of *Miohippus intermedius*. The similarity of ratios between the genera suggests that this is not a diagnostic character.

A. L/size	1	2
1. *Miohippus*	1.000	
2. *Mesohippus*	0.368	1.000
B. H/size	**1**	**2**
1. *Miohippus*	1.000	
2. *Mesohippus*	**0.038**	1.000
C. D/size	**1**	**2**
1. *Miohippus*	1.000	
2. *Mesohippus*	0.363	1.000

TABLE 5. Matrices of pairwise probabilities of mean differences L/size ratios (A), H/size ratios (B), and Depth/size ratios (C) for the preorbital fossa of specimens classically identified as *Miohippus* and *Mesohippus*. Values in bold indicate significance ($p < 0.05$) using one-way ANOVA tests. Abbreviations same as Table 3.

The articular facet of the third metatarsal and the size of the preorbital fossa appear to be related to body size. There is not enough evidence at present to keep *Mesohippus* and *Miohippus* as separate genera. I synonymize *Mesohippus* with *Miohippus*. *Miohippus* has priority over *Mesohippus*, because *Miohippus* was named before *Mesohippus* was named.

MIOHIPPUS CELER (Marsh, 1874)

Table 6

ANCHITHERIUM CELER Marsh, 1874

MESOHIPPUS CELER Marsh, 1875; Osborn, 1904, 1918; Scott, 1941; Clark and Beerbower, 1967; Kihm, 1987

MIOHIPPUS CELER Hay, 1902

MESOHIPPUS BAIRDII Osborn and Wortman, 1894 (in part)

MESOHIPPUS VIEJENSIS Clark and Beerbower, 1967 (in part)

ANCHITHERIUM WESTONI Cope, 1889

MESOHIPPUS WESTONI Osborn, 1904; Prothero and Shubin 1989 (in part)

MESOHIPPUS LATIDENS Douglass, 1903

MESOHIPPUS MONTANENSIS Osborn, 1904

MESOHIPPUS BAIRDII CELER Forstén, 1970b

MESOHIPPUS TEXANUS McGrew, 1971

Holotype—YPM 11302, a right maxillary with P4–M3; from the Chadron Formation of Nebraska.

Revised Description—Hypostyle often not present in molars, and when present it is often poorly developed. P2 is molariform, but is small in size.

Biostratigraphic Occurrences—Late Duchesnean through late Chadronian

Revised Diagnosis—*M. celer* can be distinguished from all other species of *Miohippus*

by (1) its smaller size, (2) lack of a hypostyle in some or all upper molars, and (3) proportionally small P2 length compared to the other upper cheek teeth.

Referred Specimens— Earliest Chadronian: FMNH PM 107, FMNH PM 121, FMNH 142, FMNH 151; Chadronian: YPM 11302.

Discussion—*Miohippus celer* represents the most primitive form of *Miohippus*, and may represent the ancestral condition of *Miohippus* (McGrew, 1971). All South Dakota specimens of *Mesohippus viejensis* (Clark and Beerbower, 1967) should be referred to *M. celer*. *Mesohippus texanus* (McGrew 1971), from the late Duchesnean to earliest Chadronian of Texas, is very similar to *M. celer*. McGrew (1971) stated that *M. texanus* is distinct from *M. celer (M. viejensis*) from South Dakota due to the smaller size of *M. texanus*. I have only examined the type specimen (FMNH PM 121) of *M. texanus*. *Miohippus texanus* does not seem to significantly differ in size or morphology from *M. celer*. McGrew (1971) reports a range of 8.4 mm–9.9 mm for M1 length for *M. texanus*, which is similar to the range of *M. celer*. Data from McGrew (1971) indicates that *M. texanus's* M1-3 length is greater than P2–4 length, due to the small size of P2. There is not enough data to see if this is also true in *M. celer.* Due to a lack of objective criteria separating them, I consider *Mesohippus texanus* to be a junior

		n	Min.	Max.	Mean	SE	SD	V
P1	L	1	—	—	6.03	—	—	—
	W	1	—	—	3.98	—	—	—
P2	L	1	—	—	10.10	—	—	—
	W	1	—	—	9.61	—	—	—
P3	L	1	—	—	9.98	—	—	—
	W	1	—	—	11.39	—	—	—
P4	L	2	10.05	10.39	10.22	0.17	0.24	2.35
	W	2	11.58	13.06	12.32	0.74	1.05	8.49
M1	L	2	9.63	10.43	10.03	0.40	0.57	5.64
	W	2	11.03	12.63	11.83	0.80	1.13	9.6
M2	L	1	—	—	9.38	—	—	—
	W	2	11.88	12.58	11.88	0.70	0.99	8.33
M3	L	1	—	—	9.58	—	—	—
	W	1	—	—	10.49	—	—	—
p1	L	0	—	—	—	—	—	—
	W	0	—	—	—	—	—	—
p2	L	1	—	—	8.74	—	—	—
	W	1	—	—	4.96	—	—	—
p3	L	1	—	—	9.04	—	—	—
	W	1	—	—	6.83	—	—	—
p4	L	1	—	—	9.07	—	—	—
	W	1	—	—	7.52	—	—	—
m1	L	1	—	—	8.75	—	—	—
	W	1	—	—	6.84	—	—	—
m2	L	3	8.71	9.41	9.05	0.20	0.35	3.88
	W	3	6.36	6.53	6.47	0.06	0.10	1.47
m3	L	3	11.66	12.46	12.03	0.23	0.40	3.36
	W	3	5.45	5.81	5.58	0.12	0.20	3.63

TABLE 6. Descriptive statistics for *Miohippus celer*. **Abbreviations: max.,** maximum, **min.,** minimum, **SD,** standard deviation, **SE,** standard error.

subjective synonym of *Miohippus celer*.

Osborn (1904) reported that *Mesohippus montanensis* from the middle Chadronian (Prothero and Shubin, 1989) lacks a hypostyle. The type of *Mesohippus westoni* also lacks a hypostyle (Osborn, 1904). Macdonald (1992) declared *Mesohippus montanensis* and *Mesohippus westoni* to be nomina dubia. I consider *Mesohippus montanensis* to be a junior synonym of *Miohippus celer*, due to the absence of the hypostyle and its small size. Osborn's (1904; 1918) description of *Mesohippus westoni* is similar to *Miohippus celer*. Both are 'small' horses lacking a hypostyle in the molars. Prothero and Shubin (1989) report that some *Mesohippus westoni* have a hypostyle present in all of the molars. These specimens may belong to *Miohippus bairdii*, however, because they have hypostyles in all of their molars and are similar in size. I consider all forms of *Mesohippus westoni* lacking a hypostyle in any of the molars to be considered specimens of *M. celer*.

Prothero and Emery (2004) indicate that *Mesohippus westoni* became extinct near the Chadronian–Orellan boundary, which they recognized as corresponding to the upper boundary of the Chadron Formation in Nebraska. Zanazzi et al. (2009) tentatively placed the Chadronian–Orellan boundary about 2 meters above the UPW in Nebraska, which is 6 meters below the boundary recognized by Prothero and Emery (2004). This means that taxa like *Miohippus celer*, *Miohippus grandis*, and *Brontotheriidae* may not have become extinct until until the earliest Orellan in Nebraska. I have not found any molars lacking hypostyles in the earliest Orellan material examined, but it is possible that *Miohippus celer* is found in earliest Orellan material from other states (as reported by Prothero and Shubin, 1989). Zanazzi et al. (2009) state that further sampling of Toadstool Geologic Park is needed to verify the placement of the Chadronian-Orellan boundary in Nebraska.

MIOHIPPUS BAIRDII (Leidy, 1850)

Table 7

PALAEOTHERIUM BAIRDII Leidy, 1850

ANCHITHERIUM BAIRDII Leidy, 1852, 1869

MIOHIPPUS BAIRDII Hay, 1902; Osborn, 1918; Simpson, 1985

MESOHIPPUS BAIRDI Marsh, 1875; Scott, 1891; Osborn, 1904; Prothero and Shubin, 1989

MESOHIPPUS BAIRDII Osborn and Wortman, 1895; Forstén, 1970b (in part)

MESOHIPPUS WESTONI Prothero and Shubin, 1989 (in part)

MESOHIPPUS HYPOSTYLUS Osborn, 1904; Clark and Beerbower, 1967

ANCHITHERIUM EXOLETUM Cope, 1874

MIOHIPPUS EXOLETUM Hay, 1902

MESOHIPPUS EXOLETUS Stirton, 1940; Scott, 1941; Prothero and Shubin, 1989

MESOHIPPUS TRIGONOSTYLUS Osborn, 1918

PEDIOHIPPUS TRIGONOSTYLUS Schlaikjer, 1935

Holotype—USNM 8632, partial skull with left M2-3, right M1-3, and the posterior half of the cranium; the stratigraphic level is unknown, but most likely from the Scenic Member of South Dakota (Prothero and Shubin, 1989).

Revised Description—The hypostyle is present in all molars. The third metatarsal articulation facet is undeveloped or partially developed.

Biostratigraphic Occurrences—Late early Chadronian through latest Orellan

Revised Diagnosis—*M. bairdii* is larger than *Miohippus celer* and a hypostyle is present in all upper molars, unlike *M. celer* that lacks a hypostyle in all upper molars. *Miohippus bairdii* is smaller than *Miohippus grandis*. *Miohippus bairdii* is slightly smaller than *Miohippus barbouri* and *Miohippus obliquidens*. *Miohippus bairdii* differs further in not having an anteriorly widening rostrum/mandibular symphasis as seen in *Miohippus barbouri* or obliquely orientated molars as seen in *Miohippus obliquidens*.

Referred Specimens— See Appendix A, B, C

		n	Min.	Max.	Mean	SE	SD	V
P1	L	32	6.94	9.37	7.98	0.11	0.60	7.54
	W	30	5.02	7.00	5.90	0.10	0.53	9.03
P2	L	64	10.55	13.82	12.55	0.08	0.64	5.13
	W	58	11.36	13.71	12.50	0.08	0.60	4.81
P3	L	65	10.86	13.32	12.29	0.07	0.54	4.36
	W	61	12.33	15.08	13.71	0.08	0.66	4.79
P4	L	70	11.15	13.81	12.49	0.07	0.61	4.91
	W	65	12.15	15.68	13.92	0.08	0.64	4.62
M1	L	70	10.97	13.97	12.12	0.07	0.56	4.58
	W	63	12.72	15.49	13.96	0.07	0.53	3.83
M2	L	71	10.67	13.69	12.31	0.06	0.50	4.04
	W	66	13.12	15.63	14.16	0.07	0.56	3.97
M3	L	59	10.29	12.88	11.78	0.07	0.55	4.68
	W	54	11.10	14.41	12.58	0.11	0.83	6.59
P2–4	L	30	31.19	38.05	34.73	0.25	1.37	3.95
M1–3	L	26	31.65	36.66	33.73	0.23	1.15	3.41
p1	L	9	2.92	4.24	3.58	0.15	0.45	12.59
	W	9	2.28	3.24	2.74	0.11	0.32	11.52
p2	L	45	9.35	12.66	10.87	0.11	0.71	6.57
	W	40	5.89	8.60	7.36	0.09	0.59	7.97
p3	L	67	9.53	12.45	11.16	0.08	0.64	5.78
	W	63	7.29	9.83	8.95	0.07	0.54	6.04
p4	L	75	9.92	12.28	11.17	0.07	0.57	5.09
	W	70	7.74	10.42	9.39	0.07	0.58	6.20
m1	L	74	9.42	13.14	10.83	0.07	0.61	5.63
	W	66	6.40	9.46	8.12	0.06	0.49	5.99
m2	L	78	9.78	12.65	11.23	0.06	0.56	4.99
	W	74	6.28	8.92	7.59	0.06	0.48	6.30
m3	L	83	12.59	16.59	14.60	0.08	0.74	5.09
	W	77	5.79	7.72	6.70	0.05	0.42	6.22
p2–4	L	1	—	—	34.50	—	—	—
m1–3	L	2	37.03	37.88	37.46	0.43	0.60	1.60

TABLE 7. Descriptive statistics for *Miohippus bairdii*. Abbreviations same as in Table 6.

Discussion—*Miohippus bairdii* is the most common equid found in the White River Group. Scott (1941) gave a thorough description of this species. Prothero and Shubin (1989) used the state of the hypostyle and the lingual cingulum to distinguish several similarly sized species (*Mesohippus bairdii, Mesohippus exoletus, Mesohippus westoni)*. Clark and Beerbower (1967) described the variability of these characters, and Prothero and Shubin (1989) demonstrated the variability of the hypostyle state by recognizing multiple hypostyle states within a single species. I agree with Clark and Beerbower (1967) that the lingual cingulum should not be used for taxonomic identification. The state of the hypostyle should not be used for taxonomic identification in specimens where all of the upper molars possess a hypostyle, due to its variability. The hypostyle should only be used to distinguish *Miohippus celer* from other species of *Miohippus*.

The size ranges of *Miohippus exoletus and Miohippus westoni* in Prothero and Shubin (1989) are very similar to that of *M. bairdii*, and the only anatomical differences are the hypostyle and the lingual cingulum, which are variable within a specimen. Macdonald (1992) considered *M. westoni* to be a nomen dubium. I consider *Mesohippus*

exoletus to be a junior subjective synonym of *M. bairdii*. Specimens of *Mesohippus westoni* with hypostyles present in the all of the molars may be members of *M. bairdii*.

MIOHIPPUS GRANDIS (Clark and Beerbower, 1967)

Table 8

Miohippus assiniboiensis Prothero and Shubin, 1989 (in part)

Miohippus grandis Storer and Bryant, 1993

Holotype—CM 9157, ramus with left p2–m3; from the Peanut Peak Member of the Chadron Formation of South Dakota.

Revised Description—Metatarsal cuboid facet articulation fully developed.

Biostratigraphic Occurrences—Middle Chadronian, late Chadronian

Diagnosis—Skull is longer than *Miohippus obliquidens*, but shorter than *Miohippus intermedius* (Prothero and Shubin, 1989). *Miohippus grandis* is larger than all other Chadronian and Orellan species of *Miohippus*. *Miohippus grandis* has a hypostyle in all upper molars, unlike *Miohippus celer*.

Referred Specimens— See Appendix A, B, C, D

Discussion—*Miohippus grandis* is the largest horse found in the Chadronian. Prothero and Shubin (1989) gave a thorough description of this species,

		n	Min.	Max.	Mean	SE	SD	V
P1	L	4	8.50	10.29	9.37	0.37	0.73	7.81
	W	3	5.68	7.75	6.52	0.63	1.09	16.66
P2	L	5	13.56	14.68	14.03	0.21	0.46	3.27
	W	5	13.21	14.52	13.86	0.25	0.55	3.98
P3	L	6	13.83	15.67	14.54	0.29	0.71	4.89
	W	6	14.60	16.33	15.55	0.26	0.64	4.15
P4	L	7	14.19	15.72	14.95	0.23	0.61	4.07
	W	6	14.99	16.67	15.80	0.27	0.66	4.15
M1	L	6	13.81	15.51	14.88	0.28	0.68	4.59
	W	6	15.48	17.36	16.16	0.31	0.75	4.65
M2	L	6	13.84	15.89	14.96	0.34	0.84	5.64
	W	6	15.56	18.02	16.51	0.44	1.07	6.48
M3	L	5	13.44	15.27	14.15	0.33	0.74	5.20
	W	5	12.30	16.08	14.75	0.65	1.45	9.84
P2–4	L	2	39.30	41.00	40.20	0.87	1.23	3.06
M1–3	L	1	—	—	40.60	—	—	—
p1	L	2	5.02	5.46	5.24	0.22	0.31	5.94
	W	2	2.95	3.16	3.06	0.11	0.15	4.86
p2	L	11	11.50	14.33	12.69	0.29	0.95	7.45
	W	11	7.20	8.89	8.09	0.18	0.59	7.33
p3	L	17	10.74	14.08	12.66	0.20	0.84	6.65
	W	17	7.60	10.73	9.52	0.20	0.83	8.75
p4	L	19	11.34	14.71	12.85	0.22	0.94	7.31
	W	19	7.55	11.45	10.00	0.21	0.93	9.31
m1	L	18	11.37	14.03	12.77	0.19	0.79	6.17
	W	15	8.12	9.93	9.02	0.14	0.53	5.83
m2	L	18	11.97	15.08	13.30	0.21	0.90	6.74
	W	16	7.68	9.53	8.60	0.15	0.60	7.02
m3	L	20	15.90	18.69	17.19	0.18	0.82	4.80
	W	19	6.50	8.80	7.46	0.14	0.61	8.22

TABLE 8. Descriptive statistics for *Miohippus grandis*. Abbreviations same as in Table 6.

though they mistakenly described it as *Miohippus assiniboiensis*. Storer and Bryant (1993) pointed out that *M. assiniboiensis* (Lambe, 1905) is from the late Whitneyan or Arikareean and contended that the large horse found in the Chadronian should be referred to *M. grandis*. As was the case with *Miohippus celer*, the change in the location of the Chadronian–Orellan boundary in Nebraska suggests that *M. grandis* may not terminate until the earliest Orellan. However, I have found no mandibles from earliest Orellan material that fall in the size range of *M. grandis*. Samples of m3s from the earliest Orellan of Nebraska do fall into the size range of *M. grandis*. However, m3 size is variable, so it is possible that the m3s may be from another species.

MIOHIPPUS BARBOURI (Schlaikjer, 1931)

Table 9

MEOSHIPPUS BARBOURI Schlaikjer, 1931; Prothero and Shubin, 1989

MESOHIPPUS ANTIQUUS Forsten, 1974 (in part)

Holotype—MCZ 17641, a complete skeleton from the late Orellan of the Big Badlands of South Dakota.

Revised Description—Short rostrum pinched at the diastema and widening anteriorly at the incisors, mirrored by an anteriorly widening mandibular symphasis (Fig. 13). Incisors are circular and cupped. The humerus and femur are relatively short compared to metapodial length (Prothero and Shubin, 1989).

Biostratigraphic Occurrences—Late early Orellan through latest Orellan

Revised Diagnosis—*Miohippus barbouri* can be distinguished from other Chadronian and Orellan species by a transversely broader premaxillary/mandibular symphasis (flaring symphasis of Prothero and Shubin (1989)). *Miohippus barbouri* is slightly larger than *Miohippus bairdii*, and is similar in size to *Miohippus obliquidens*. *Miohippus barbouri* differs further in not having obliquely orientated molars as seen in *M. obliquidens*.

Referred Specimens— See Appendix A, B, C

		n	Min.	Max.	Mean	SE	SD	V
P1	L	10	6.36	9.78	7.85	0.28	0.90	11.44
	W	9	5.12	6.63	5.66	0.15	0.45	7.90
P2	L	14	11.79	14.01	13.05	0.18	0.67	5.13
	W	13	11.38	13.59	12.72	0.19	0.69	5.41
P3	L	17	11.91	14.35	13.29	0.13	0.55	4.14
	W	16	12.79	14.98	14.22	0.14	0.56	3.95
P4	L	18	11.83	14.73	13.41	0.14	0.59	4.41
	W	17	13.39	15.60	14.53	0.16	0.67	4.63
M1	L	18	12.14	14.76	13.38	0.14	0.58	4.35
	W	17	13.34	15.73	14.66	0.16	0.65	4.42
M2	L	18	11.99	14.54	13.43	0.16	0.66	4.94
	W	17	13.18	15.73	14.81	0.17	0.69	4.69
M3	L	10	10.95	13.65	12.41	0.27	0.85	6.83
	W	8	11.47	13.99	12.92	0.31	0.87	6.76
P2–4	L	8	35.17	37.99	36.84	0.37	1.04	2.83
M1–3	L	6	34.03	38.03	36.09	0.62	1.52	4.22
p1	L	3	2.86	3.52	3.26	0.20	0.35	10.74
	W	3	2.36	2.75	2.52	0.12	0.20	8.11
p2	L	11	9.80	15.66	11.39	0.48	1.61	14.11
	W	11	6.92	9.40	7.97	0.24	0.80	10.03
p3	L	18	10.18	14.58	11.72	0.25	1.05	8.97
	W	16	8.13	11.26	9.41	0.22	0.86	9.16
p4	L	18	10.47	14.63	11.92	0.22	0.93	7.83
	W	16	8.78	11.60	9.71	0.20	0.80	8.27
m1	L	23	10.22	15.05	11.90	0.23	1.08	9.07
	W	20	7.61	10.38	8.55	0.14	0.64	7.51
m2	L	22	10.20	15.63	12.05	0.24	1.14	9.42
	W	22	6.71	9.50	7.99	0.13	0.62	7.72
m3	L	20	13.29	17.37	15.93	0.20	0.90	5.62
	W	20	5.83	7.85	6.92	0.10	0.44	6.43

TABLE 9. Descriptive statistics for *Miohippus barbouri*. Abbreviations same as in Table 6.

Discussion— The transversely broad premaxillary/mandibular symphasis is an important identifying feature of *Miohippus barbouri*. The transversely broad premaxillary/mandibular symphasis is present in juvenile and adult specimens, indicating that it is not a result of old age. *Miohippus barbouri* is one of the larger species of horse found in the Orellan. Prothero and Shubin (1989) reported a smaller size for *M. barbouri,* though some specimens in the UNSM, SDSM, or FMNH collections are larger than their size range and possess a transversely broad premaxillary/mandibular symphasis. No specimens observed had obliquely oriented molars, which is a major characteristic for *Miohippus obliquidens*, which is also in the same size range. Analysis of the data reveals that in some specimens of *M. barbouri* M1-3 length is greater than P2–4 length (Fig. 14). Prothero and Shubin (1989) demonstrate that *Mesohippus westoni*, *M. barbouri,* and *Miohippus obliquidens* have a P2–4 length greater than M1-3 length.

The type of *M. barbouri* lacks an articular facet on the third metatarsal (Schlaikjer, 1932). Forsten (1974) reported that there are 11 third metatarsals of *M. antiquus* from the Harvard Fossil Reserve in Goshen County, Wyoming. Nine of these metatarsals have a fully developed articular facet, while two of them lack an articular

FIGURE 13. Lower jaw of *Miohippus barbouri*. The mandibular symphasis widens anteriorly and the incisors are deep and cupped.

facet or have a poorly developed facet. Prothero and Shubin (1989) assumed that the developed articular facets belong to *M. obliquidens* and that the undeveloped articular facets belong to *M. barbouri*. Forsten (1974) does not mention if any of these metatarsals are associated with cranial elements. If the articular facet of the third metatarsal is related to body size then it can be expected that large forms of *M. barbouri* would have a developed or partially developed articular facet, and the smaller forms would have an undeveloped or partially developed articular facet. Schlaikjer's (1932) measurements indicate that the type specimen of *M. barbouri* was a small individual. Without associated cranial or dental material the 11

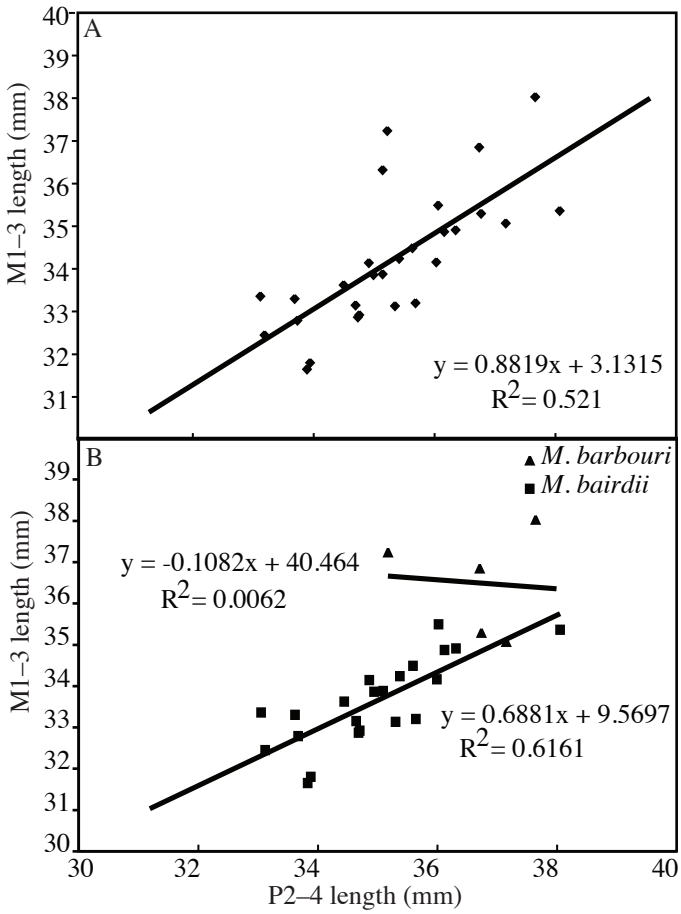

FIGURE 14. Graphs displaying P2–4 length and M1–3 length. Graph A displays the measurements of all horses, and Graph B dispalys *Miohippus bairdii* vs. *Miohippus barbouri*. Some *Miohippus barbouri* have a larger M1–3 length than P2–4 length.

third metatarsals of Forsten (1974) cannot be placed into a species. Unfortunately no specimen of *M. barbouri* observed in this study had an associated third metatarsal.

Miohippus obliquidens and *M. barbouri* are similar in size and both have a M1-3 length greater than P2–4 length. The main differences between these taxa are the obliquely oriented molars of *M. obliquidens* and the transversely broader premaxillary/ mandibular symphasis of *M. barbouri*. As stated above, I saw no specimens in the UNSM, SDSM, or FMNH collections with the obliquely oriented molars of *M. obliquidens*, and a direct comparison was not possible. Further analysis is needed to verify if these taxa should remain distinct.

DISCUSSION

Implications for Equid Evolution

Interpretations made here have important implications for understanding equid evolution. *Miohippus* coexists with *Epihippus* and *Haplohippus* in the Duchesnean and *Kalobatipus*, *Archaeohippus*, and *Parahippus* in the Arikareean, but for most of its existence it is the lone equid genus (MacFadden, 1998). The late early Chadronain to Whitneyan represents a period of relative homogeneity for horses. Yet several key features shared by all younger equid genera are derived in this period. *Miohippus* has reached a weight threshold and has begun to shift its weight distribution to the central digit of the hind limb. It is well documented that the larger species classically identified as *Miohippus* have a developed articular facet, which is a product of shifting weight onto the third metatarsal. Yet smaller species classically identified as *Mesohippus* are also redistributing their weight, seen in partially developed articular facets. The difference in orientation angle between the partially developed facet and the developed facet implies

a difference in the amount of weight transferred to the third metatarsal. The low angle and larger surface area of the developed facet allows a greater amount of weight to be transferred to the third metatarsal than in the partially developed facet.

The second character derived by *Miohippus* is the hypostyle. The hypostyle occludes with the parastylid of the posterior lower tooth, M1/m2 and M2/m3, or with the hypoconulid, M3/m3, and provides additional grinding surface. *Miohippus celer* possess a hypostyle in some individuals, yet its presence is variable. All other species possess a hypostyle in each molar, though the shape varies among teeth in an individual. The hypostyle joins the metastyle with the metaloph and hypocone in younger genera. This forms the more complex lophodonty seen in later hypsodont horses. The development of these two characters in *Miohippus* is part of the evolutionary transition of the small, generalized forms of older genera into the larger, specialized forms seen in younger genera.

During this study I tried to establish lineages through the biozones (Fig. 15). Some branches were distinct throughout the interval sampled. *Miohippus bairdii* stays fairly constant in size over time, as there are no significant differences among populations from different biozones between the states (Table 2). In South Dakota the middle Chadronian population of *M. bairdii* is significantly different from the populations of *M. bairdii* in the Orellan (Table 2). However, this population has very few samples (n=3) and one M1 length is an outlier. When this measurement is removed, there is no longer a significant difference between these populations. The South Dakota middle Chadronian population of *M. bairdii* is not significantly different from the South Dakota Chadronian population of *Miohippus grandis* (n=4). However, when the outlier is removed, the difference between the two populations becomes significant. In the late Chadronian there are two 'small' species, *M. celer* and *M. bairdii*, and one 'large' species, *M. grandis*. In the Orellan there is one 'small' species, *M. bairdii*, and two 'large' species, *M. barbouri* and *M. obliquidens*. Further analysis of *M. celer* and *M. obliquidens* is needed to

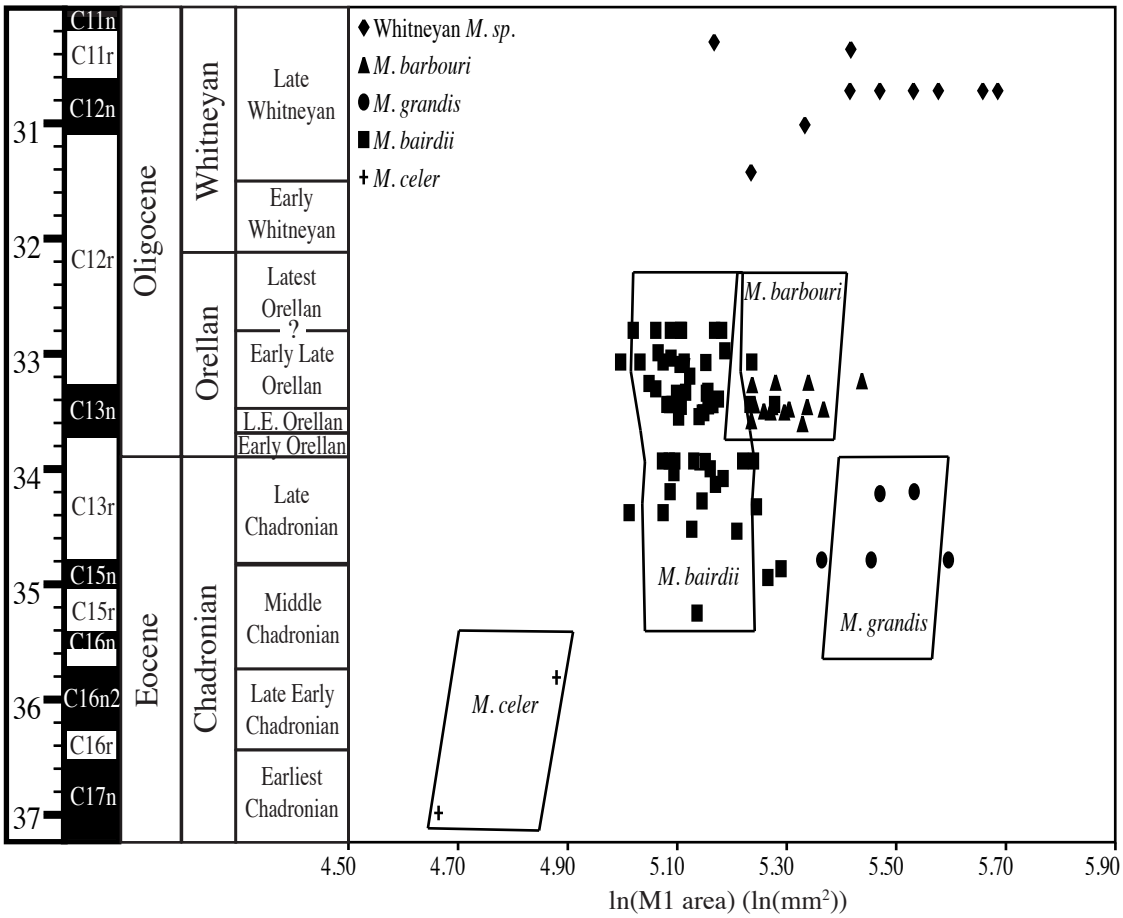

FIGURE 15. Proposed lineages for *Miohippus* using natural log of M1 area. Size ranges are ± 0.1 from the mean. This is the amount of variation expected in a species (Gingerich et al., 1982). Magnetostratigraphy: Swisher and Prothero (1990); Prothero and Swisher (1992); Ogg and Smith (2004). Biostratigraphy: Prothero and Whittlesey (1998); Prothero and Emery (2004).

establish better-defined evolutionary lineages.

CONCLUSIONS

I consider *Mesohippus* to be a junior synonym of *Miohippus* due to a lack of objective criteria separating these genera. Some authors have suggested that the presence of the articular facet on the third metatarsal is an important character separating these genera, but the presence of partially developed facets in smaller forms removes the

usefulness of this character for generic distinction.

I recognize *Miohippus celer*, *Miohippus bairdii*, *Miohippus grandis*, and *Miohippus barbouri* in the Chadronian and Orellan White River deposits in Nebraska and South Dakota. *Miohippus celer*, *Miohippus bairdii*, and *Miohippus grandis* coexist in the Chadronian, while *Miohippus bairdii* and *Miohippus barbouri* coexist in the Orellan. At least three lineages are implied. This period of relative homogeneity in equids is an important period of equid evolution, as several derived characters seen in younger, more specialized genera first appear.

This study did not include the large sample of White River equids curated at the American Museum of Natural History. Future study of this collection and other material can serve as a test of the species divisions proposed here. Larger samples of *Miohippus celer* are needed to understand its relationship to other species. Additional specimens of *Miohippus* from the Whitneyan and Arikareean also need to be examined to test the validity of established species in these land-mammal ages.

ACKNOWLEDGEMENTS

I would like to thank the University of Nebraska-Lincoln Department of Geosciences, the Nebraska Geological Society and AAPG for providing financial support; B. Simpson and the Chicago Field Museum of Natural History for access to specimens; S. Shelton and the South Dakota School of Mines and Technology Museum of Geology for access to specimens; R. Secord, R. Hunt, M. Joeckel, and D. Loope for being members of my committee; R. Secord and R. Hunt for advice and corrections while writing this manuscript; G. Corner for help in the University of Nebraska State Museum; G. Brown, R. Skolnick, and E. Stepleton for preparation of specimens; A. Fox and R. Secord for advice on designing figures; E. Evanoff and H. Minkler for their

correspondences. I also want to thank all of my professors who have helped me along the way. The knowledge that they imparted to me and the patience they showed me were invaluable. Thank you to the employees of the Vertebrate Paleontology Division of the University of Nebraska State Museum for helping me with my project and instilling in me a greater love and understanding of vertebrate paleontology.

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APPENDIX A

UPPER CHEEK TOOTH MEASUREMENTS

All tooth measurements in Appendix A are in units of millimeters (mm). Stratigraphic level is reported in meters (m) and refers to FIGURE XX. For specimens from Nebraska 0 m is the UPW, as in Zanazzi et al. (2009). In South Dakota 0 m is the base of the Ahearn Member of the Chadron Formation. Stratigraphic level in bold indicates the specimen is from a stratigraphic range and the average value is reported. Specimen numbers in bold indicates that both the left and right tooth rows of an individual were measured and the average value of all tooth measurements is reported. For biozone information, refer to the following abbreviations:

NE	Nebraska
OR	Oregon
SD	South Dakota
TX	Texas
Ar–1	Early Arikareean
Wh–2	*Merycoidodon major* Zone (Late Whitneyan)
Wh–1	*Leptauchenia major* Zone (Early Whitneyan)
Or–4	*Meycoidodon bullatus* Zone (Latest Orellan)
Or–3	*Miniochoerus gracilis* Zone (Early Late Orellan)
Or–2	*Miniochoerus affinis* Zone (Late Early Orellan)
Or–1	*Hypertragulus calcaratus* Zone (Earliest Orellan)
Ch–4	*Miniochoerus chadronensis* Zone (Late Chadronian)
Ch–3	*Leptomeryx mammifer* Zone (Middle Chadronian)
Ch–2	*Leptomeryx yoderi* Zone (Late Early Chadronian)
Ch–1	*Bathygenys* Zone (Earliest Chadronian)

TABLE A1

Biozone	Locality	Strat Level	Age	Species	Specimen #	P1L	P1W	P2L	P2W	P3L	P3W	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W
OR Ar-1				*M. acutidens*	**UCMP 376**	9.70	6.15	13.54	13.97	13.18	15.40	13.43	15.26	12.55	15.37	13.63	15.99	12.98	13.01
OR Ar-1				*M. annectens*	**YPM 11275**	11.36	8.60	18.93	18.15	17.88	19.52							15.47	16.58
NE Wh–2	SX-15	91.1	31.50	*M. sp.*	**UNSM 131709**			12.67	13.19	12.68	14.71	12.52	15.33	12.77	14.70			12.39	12.78
SD Wh–2		187.8	30.81	*M. intermedius*	**AMNH 1196**			15.58	15.02	15.44	16.92	16.06	17.47	14.80	17.61	15.75	17.24	14.54	15.23
SD Wh–2		**207.2**	30.46	*M. sp.*	FMNH PM 25930			15.63	14.00	14.86	15.09	15.21	16.80	14.36	15.68	14.92	16.06	13.97	14.36
SD Wh–2		**187.8**	30.81	*M. sp.*	**SDSM 284**	10.71	7.02	16.03	15.69	16.42	17.19	17.04	17.79	16.61	17.74	17.04	18.62	14.98	15.77
SD Wh–2	V401	**187.8**	30.81	*M. sp.*	SDSM 29101											16.70	16.98	14.71	16.38
SD Wh–2	V401	**187.8**	30.81	*M. sp.*	**SDSM 2972**	10.53	7.18	16.25	15.58	16.17	17.33	16.36	17.89	16.07	17.84	15.84	18.26	14.82	16.08
SD Wh–2	V401	**187.8**	30.81	*M. sp.*	**SDSM 40125**			14.92	15.93	14.86	16.48	15.39	16.88	13.77	16.33	15.23	17.12	13.84	14.13
SD Wh–2	V401	**187.8**	30.81	*M. sp.*	**SDSM 40134**	9.40	6.19	15.63	15.02	15.23	16.34	14.81	16.73	14.28	16.63			13.84	14.56
SD Wh–2	V401	**187.8**	30.81	*M. sp.*	**SDSM 40147**			14.61	15.36	15.05	16.97	14.99	16.75	15.31	17.26	14.10	17.53	14.34	15.20
SD Wh–2	V401	**187.8**	30.81	*M. sp.*	**SDSM 4094**					16.73	16.75	15.80	17.45	15.10	16.72	15.08	17.20	14.20	14.93
SD Wh–2	V712	209.1	30.40	*M. sp.*	SDSM 58294													16.33	16.65
SD Wh–2	V712	**187.8**	31.10	*M. sp.*	**SDSM 58298**									13.85	14.95	14.04	15.23		
SD Wh–2	V6910	**172.8**	31.10	*M. sp.*	SDSM 72297	7.91	5.28	11.73	11.74	11.50	13.34								
SD Wh–2	V712	**209.1**	30.40	*M. sp.*	SDSM 73740			12.10	11.62	11.66	13.36	11.88	13.81	12.19	14.39	12.28	14.36	12.47	
NE Or–4	SX-26	31.0	33.12	*M. bairdii*	UNSM 131632			12.97	12.42	12.83	13.84	13.09	14.04	12.40	13.94	12.78	14.45	11.77	12.81
NE Or–4	SX-17	30.5	33.14	*M. bairdii*	**UNSM 131633**					11.36	13.24	12.13	13.48	12.12	13.62	13.05	13.73	11.16	11.39
NE Or–4	SX-4	34.1	33.04	*M. bairdii*	**UNSM 131667**	7.73	5.75	12.74	13.17	11.86	15.08	12.53	15.07	11.16	14.20	11.42	15.19	11.71	13.67
NE Or–4	SX-3	32.4	33.09	*M. bairdii*	**UNSM 131692**	8.31	7.00	12.15	11.88	12.01	13.40	12.66	13.60	12.16	13.36	11.25	13.23	10.64	11.12
NE Or–4		34.8	33.02	*M. bairdii*	**UNSM 131714**			13.54	13.36	13.01	14.12	13.09	14.76	12.55	14.26	12.49	14.63		
NE Or–4	SX-?	31.4	33.11	*M. barbouri*	UNSM 131699			12.51	13.59	13.02	14.53	13.11	15.04			13.24	15.07		
NE Or–3	SX-39	21.7	33.37	*M. bairdii*	**UNSM 131538**			12.84	12.62	13.20	14.03	12.93	14.05	11.97	13.88	11.90	14.57	11.22	13.02
NE Or–3	SX-37	19.5	33.43	*M. bairdii*	**UNSM 131540**	8.13	6.85	13.31	12.76	12.91	13.95	12.67	14.21	12.60	14.04	12.29	13.77	11.25	12.03
NE Or–3	SX-4	26.7	33.24	*M. bairdii*	**UNSM 131543**	8.27	6.21	13.02	13.62	12.64	14.73	13.02	14.73	11.58	14.51	11.83	14.36	12.61	12.86
NE Or–3	SX-26	21.4	33.38	*M. bairdii*	**UNSM 131546**	7.50	5.51	12.42	12.54	11.78	13.68	12.47	13.99	12.34	14.02	13.07	14.33	11.62	12.19
NE Or–3	SX-26	15.3	33.55	*M. bairdii*	**UNSM 131598**	8.37	5.89	12.58	12.54	12.43	13.88	12.60	14.15	12.24	14.07	12.21	14.22	11.42	
NE Or–3	SX-6	18.0	33.47	*M. bairdii*	UNSM 131602			11.49	11.47	11.22	13.10	11.46	13.50						
NE Or–3	SX-4a	17.1	33.49	*M. bairdii*	**UNSM 131615**	7.12	5.02	13.06	12.95	11.67	14.10	12.52	14.54	12.35	14.08	12.55	14.43	11.87	12.05
NE Or–3	SX-6	13.8	33.59	*M. bairdii*	**UNSM 131619**			12.25	13.36	12.53	14.41	12.47	14.18	11.67	13.96	11.92	14.34	11.86	12.41
NE Or–3	SX-6	18.0	33.47	*M. bairdii*	UNSM 131620					12.20	14.21	11.73	14.26	12.14	14.30	12.38			
NE Or–3	SX-6	**14.0**	33.58	*M. bairdii*	UNSM 131631							13.33	13.94	12.16	14.04	12.40	14.09	11.64	11.90
NE Or–3	DW-?	24.5	33.30	*M. bairdii*	UNSM 131634			12.75	12.33	12.27	12.73	12.70	13.08	12.25	12.72	12.30	13.12		
NE Or–3	SX-25	24.5	33.30	*M. bairdii*	UNSM 131639											11.72	13.63	11.24	12.49
NE Or–3	SX-19	22.0	33.37	*M. bairdii*	**UNSM 131668**	7.87	5.06	13.30	12.67	12.83	14.01	12.64	13.66	12.39	14.01	11.89	14.22	12.70	13.44
NE Or–3	SX-6	24.5	33.30	*M. bairdii*	UNSM 131679			12.90		12.60		12.66		12.01		12.63		12.70	
NE Or–3	DW-104	25.0	33.29	*M. barbouri*	UNSM 131515	7.49	5.90	13.60	13.41	14.35	14.93	13.81	15.47	13.58	15.35	13.99	15.73	13.15	13.58

Biozone	Locality	Strat Level	Age	Species	Specimen #	P1L	P1W	P2L	P2W	P3L	P3W	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W
NE Or–3	SX-26	15.6	33.54	*M. barbouri*	UNSM 131534	7.94	5.93	12.50	11.98	13.48	14.56	14.73	14.57	13.84	14.42	13.74	14.50	13.29	
NE Or–3	SX-26	15.6	33.54	*M. barbouri*	UNSM 131535	8.14	5.59	12.30	12.90	12.94	14.69	13.65	14.97	13.14	14.80	14.54	15.35	13.65	13.70
NE Or–3	SX-4	**16.4**	33.52	*M. barbouri*	UNSM 131611					13.58	13.99	14.21	13.81	14.10	14.27	13.60	14.60		
NE Or–3	SX-24	15.8	33.53	*M. barbouri*	UNSM 131621	8.26	5.60	13.79	13.22	13.37	14.98	13.64	15.60	13.18	14.58	13.67	15.18		
NE Or–3	SX-1	25.4	33.28	*M. barbouri*	UNSM 131635									14.76	15.57	14.53	15.43		
NE Or–3	SX-12	24.9	33.29	*M. barbouri*	UNSM 131688			13.68	13.37	12.83	14.39	13.50	14.91	13.53	14.51	13.73	14.79	12.78	
NE Or–3	SX-12	**24.1**	33.31	*M. barbouri*	UNSM 131704	7.81	5.47	13.30	13.12	13.29	14.15	13.44	14.54	12.88	14.61	13.33	15.03	11.76	13.33
NE Or–3	SX-37	16.5	33.52	*M. barbouri*	UNSM 131722							13.55	15.43	13.62	15.73	12.78	14.99	10.95	12.36
SD Or–3		**68.8**	33.12	*M. bairdii*	FMNH PM 14941			12.21				12.56		11.82	14.06			10.29	11.80
SD Or–3		**68.8**	33.12	*M. bairdii*	**FMNH PM 14944**	7.76	6.34	13.12	13.20	12.30	14.74	12.69	14.96	11.18	14.31	12.71	14.80	12.44	13.52
SD Or–3		**68.8**	33.12	*M. bairdii*	FMNH PM 14945	8.32	6.20	12.87	13.25	12.74	14.60	12.96	15.68	12.35	15.22	12.56	14.47	12.02	14.41
SD Or–3		**68.8**	33.12	*M. bairdii*	**FMNH PM 14946**	8.88	5.71	12.27	12.37	11.68	13.54	11.73	13.79	11.28	13.60	11.67	13.57	11.62	12.33
SD Or–3		**78.2**	32.85	*M. bairdii*	**FMNH PM 21006**	8.07	5.98	12.12	11.36	11.64	12.52	11.63	12.75	12.08	13.67	12.29	13.79	11.71	12.09
SD Or–3		**68.8**	33.12	*M. bairdii*	FMNH PM 9268			12.09	12.52	12.01	13.73	11.70	13.68	11.47	12.90	12.26	14.15	11.83	12.24
SD Or–3	V2001-04	**78.2**	32.85	*M. bairdii*	SDSM 58469			11.83	11.64	12.98	12.33								
SD Or–3	V2001-06	**78.2**	32.85	*M. bairdii*	SDSM 59569	8.11	5.71	12.08	11.87	12.11	13.42	11.98	13.63	11.95	13.56	12.00	13.49	11.49	12.09
SD Or–3	V7723	**78.2**	32.85	*M. bairdii*	SDSM 60996			12.67	11.92	12.60	13.15	12.66	13.12	12.97	13.72	12.65	13.83		
SD Or–3	V7723	**78.2**	32.85	*M. bairdii*	SDSM 60997			13.06	11.62	12.23	12.87	11.70	12.72	12.64	13.08	12.30	13.28		
SD Or–3	V2002-27	**78.2**	32.85	*M. bairdii*	**SDSM 69083**			12.77	11.96	12.29	13.13	12.78	13.43	12.76	13.77	12.90	14.21		
SD Or–3	V2001-06	**78.2**	32.85	*M. bairdii*	**SDSM 69735**			11.27	11.40	11.49	12.38	11.72	12.52	11.91	13.25	12.63	13.71	12.03	12.35
SD Or–3	V708	**78.2**	32.85	*M. bairdii*	**SDSM 73240**			12.11	11.87	11.99	13.31	12.13	13.53	11.23	13.48	11.96	14.05	10.96	11.87
NE Or–2	SX-24	11.6	33.65	*M. bairdii*	UNSM 131601					11.95	14.43					11.46	15.16	11.73	12.65
NE Or–2	SX-19	11.9	33.64	*M. barbouri*	UNSM 131539	9.78		13.59		13.69		13.29		13.63		13.40			
NE Or–2	SX-11	11.9	33.64	*M. barbouri*	UNSM 131545			14.01	12.41	13.81	14.49	13.46	14.60	13.91	14.83	13.82	15.52		
NE Or–2	SX-17	12.8	33.61	*M. barbouri*	UNSM 131597					13.70	13.84	13.26	14.32	12.98	14.47	13.44	14.94		
SD Or–2		**56.0**	33.48	*M. bairdii*	FMNH P 12855			12.09	12.32	12.30	12.81	11.88	13.17			11.92	13.29	10.68	11.32
SD Or–2		**56.0**	33.48	*M. bairdii*	**FMNH PM 14417**			12.11	12.98	12.13	13.61	11.81	13.92			11.89	14.05	11.48	12.23
SD Or–2		**56.0**	33.48	*M. bairdii*	FMNH PM 22142	7.35	6.27	12.51	12.49	11.93	13.50	11.44	14.14	11.80	13.97	12.41	14.10	11.84	12.67
SD Or–2		**56.0**	33.48	*M. bairdii*	FMNH PM 43249			13.15	13.24	13.20	14.01	12.85	12.15	12.30	13.76				
SD Or–2		**56.0**	33.48	*M. bairdii*	FMNH PM 43271			13.81	12.27			13.29	14.14	11.44	14.22	12.74	13.71	11.88	11.90
SD Or–2		59.3	33.38	*M. bairdii*	**FMNH PM 55668**	8.31	6.37	12.80	11.90	12.36	12.94	13.04	13.60	12.12	13.53	12.05	13.84	11.89	12.80
SD Or–2		**56.0**	33.48	*M. bairdii*	FMNH PM 8892									12.32	14.21	12.58	14.00	12.04	12.62
SD Or–2		**56.0**	33.48	*M. bairdii*	**FMNH PM 9296**			12.41	13.35	12.60	14.75	12.52	14.62	12.23	14.25	12.41	14.57	12.52	13.37
SD Or–2	V242	**56.0**	33.48	*M. bairdii*	SDSM 424	8.41		13.82		12.85		13.66		11.83		11.75		11.76	
SD Or–2	V9626	**56.0**	33.48	*M. bairdii*	**SDSM 48598**	8.37	6.64	11.58	12.20	12.20	13.50	12.12	13.54	12.59	13.82	12.48	13.86	11.47	11.60
SD Or–2	V9626	**56.0**	33.48	*M. bairdii*	SDSM 48753			12.66	12.13	12.57	12.86	12.68	13.21						
SD Or–2	V6105	**56.0**	33.48	*M. bairdii*	**SDSM 5080**	8.83	5.98	13.48	13.71	12.66	14.62	12.18	14.27	11.48	14.35	12.34	14.14	11.12	12.45

Biozone	Locality	Strat Level	Age	Species	Specimen #	P1L	P1W	P2L	P2W	P3L	P3W	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W
SD Or–2	V6105	**56.0**	33.48	*M. bairdii*	**SDSM 5811**	6.94	5.19	11.52	12.57	11.79	13.68	11.74	13.35	11.87	13.57	12.05	13.32	11.61	11.10
SD Or–2	V6027	**56.0**	33.48	*M. bairdii*	SDSM 59149							12.29	14.24	12.73	14.72	12.88	14.50	12.33	13.97
SD Or–2	V6027	**56.0**	33.48	*M. bairdii*	SDSM 59153	9.37		11.98		11.92		12.82		12.51		12.65		11.38	
SD Or–2		**56.0**	33.48	*M. bairdii*	SDSM 6137	8.38	5.65	12.78	12.42	12.66	13.82	11.70	13.88	12.02	13.50	12.22	13.25	10.84	11.71
SD Or–2	V9626	**56.0**	33.48	*M. bairdii*	**SDSM 62209**							13.70	14.97	12.67	15.49	12.47	15.63	12.88	13.25
SD Or–2	V273	60.7	33.34	*M. bairdii*	SDSM 65150	8.48	5.99	11.86		12.65	13.13	12.98	13.55	11.80	13.37			12.14	11.83
SD Or–2	V9310	55.3	33.50	*M. bairdii*	**SDSM 94CPG214**	6.94	5.11	11.43	11.75	11.63	13.35	11.72	14.03	11.35	14.64	11.71	15.00	11.51	12.32
SD Or–2		**56.0**	33.48	*M. barbouri*	FMNH PM 9858			13.12	12.26	13.28	13.73	13.07	13.63	12.91	13.55	12.21	13.18	11.90	11.47
SD Or–2	V9310	55.3	33.50	*M. barbouri*	SDSM 02CPG0-25	6.36	5.26	12.31	11.38	12.59	13.49	13.28	13.58	13.13	14.87	13.60	15.08	12.77	13.99
SD Or–2	V242	**56.0**	33.48	*M. barbouri*	SDSM 2920	7.30	5.48	11.79	11.84	11.91	12.79	11.83	13.39	12.14	13.34	11.99	13.32	11.87	12.19
SD Or–2	V361	**56.0**	33.48	*M. barbouri*	SDSM 3647	7.19	5.12	13.06	12.90	13.08	14.14	13.23	14.23	12.82	14.70	13.05	14.77	11.94	12.71
SD Or–2	V9310	55.3	33.50	*M. barbouri*	SDSM 39312	8.28	6.63	13.09	13.06	13.46	14.28	13.58	14.76	13.44	15.47				
SD Or–2	V2000-89	**56.0**	33.48	*M. barbouri*	SDSM 60306					13.63	14.50	12.76	14.23	13.33	14.16	13.09	14.25		
NE Or–1	SX-17	**5.0**	33.96	*M. bairdii*	**UNSM 131530**	8.77	6.08	12.21	12.05	12.05	13.31	12.11	13.42	11.86	13.78	11.85	13.87	11.98	12.43
NE Or–1	SX-11	4.9	33.96	*M. bairdii*	**UNSM 131537**	8.17	5.36	13.31	13.05	13.28	14.40	13.16	14.39	12.22	14.14	12.69	14.08	12.06	13.05
NE Or–1	SX-40	2.1	34.11	*M. bairdii*	UNSM 131541	8.18	6.63	13.31	13.20	12.77	14.43	13.44	14.51	12.36	14.43	13.16	15.15	11.84	13.26
NE Or–1	SX-11/12	**5.0**	33.96	*M. bairdii*	UNSM 131551			12.68	12.35	12.34	13.77	12.83	13.73	11.86	13.63				
NE Or–1	SX-25	5.5	33.93	*M. bairdii*	**UNSM 131571**			12.31	12.90	12.11	14.42	12.42	14.47	11.37		12.35	14.50	12.15	12.90
NE Or–1	SX-26	**3.1**	34.06	*M. bairdii*	UNSM 131572	7.68	6.02	12.17	13.18			12.91	13.89	11.86	13.75	12.64	14.81		
NE Or–1	SX-25	**5.0**	33.96	*M. bairdii*	UNSM 131573			12.25	12.66			12.58	14.07	11.55	13.83	11.64	13.96	11.47	12.31
NE Or–1	Sx-18	**5.0**	33.96	*M. bairdii*	UNSM 131574			13.19	12.62	13.32	13.88	13.34	14.04	13.24	14.24	12.73	14.12		
NE Or–1	SX-9	**5.0**	33.96	*M. bairdii*	UNSM 131576									12.52	14.77	12.10	13.25		
NE Or–1	SX-11	**5.0**	33.96	*M. bairdii*	UNSM 131578			10.55	11.83	10.86	13.32	11.15	14.08	10.97		10.67	14.25		
NE Or–1	SX-12	7.0	33.85	*M. bairdii*	**UNSM 131580**			12.00	12.89	11.73	13.85	11.96	13.94	11.97		11.75	14.11	11.89	12.12
NE Or–1	SX-18	**5.0**	33.96	*M. bairdii*	UNSM 131659							12.53	13.79	12.19	13.87	12.29	14.10	12.08	12.73
NE Ch–4	SX-39	-2.4	34.35	*M. bairdii*	UNSM 131510					12.71	14.26			12.52	15.14	13.69	15.24	12.58	13.79
NE Ch–4	DW-104	-1.5	34.30	*M. bairdii*	UNSM 131529	7.34	5.96	12.57	13.37	12.64	14.03	12.18	14.06	12.28	13.98	12.32	14.50	12.30	13.61
NE Ch–4	SX-26	1.2	34.16	*M. bairdii*	**UNSM 131575**									12.67	13.89	12.71	14.02		
NE Ch–4	SX-18	0.0	34.22	*M. bairdii*	UNSM 131577			13.27	12.51	12.38	13.47	12.88	13.93	12.16	13.32	12.54	14.47		
NE Ch–4	Loc. 32	0.0	34.22	*M. bairdii*	**UNSM 131684**	7.47	5.46	12.60		12.36		12.64		11.52		11.93		11.99	
NE Ch–4		**-6.1**	34.54	*M. bairdii*	UNSM 131721			11.75	11.65	11.58	13.37	12.12	13.53	12.15	13.87	12.58	14.22	11.67	11.80
NE Ch–4		-6.4	34.56	*M. bairdii*	UNSM 48485	7.32	5.73	12.75	11.82	12.98	13.84	13.62	14.35	13.47	13.58	13.13	13.33	12.18	12.54
NE Ch–4	SX-?	-8.2	34.65	*M. grandis*	FMNH PM 49935	9.33		14.27	14.52	14.75	16.33	14.95	16.30						
NE Ch–4	SX-18	0.0	34.22	*M. grandis*	**UNSM 131514**	10.29	7.75	14.68	14.28	14.93	15.42	14.91	15.73	15.48	16.35	15.39	15.79		
NE Ch–4	SX-0	-0.3	34.24	*M. grandis*	**UNSM 131517**	8.50	5.68	14.02	13.86	14.15	16.07	15.01	16.67	14.29	16.62	15.09	17.72	15.27	16.08
SD Ch–4		**44.1**	34.40	*M. bairdii*	FMNH PM 14446					12.61	12.63	11.61	13.58	11.78	13.57	12.43	14.71	12.34	14.23
SD Ch–4		**44.1**	34.40	*M. bairdii*	FMNH PM 20748											12.66	14.52	12.47	14.26

Biozone	Locality	Strat Level	Age	Species	Specimen #	P1L	P1W	P2L	P2W	P3L	P3W	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W
SD Ch–4		**44.1**	34.40	*M. bairdii*	**FMNH PM 21007**	7.20	6.24	12.75	12.41	11.93	12.90	11.85	13.11	11.30	13.31	11.99	13.47	10.78	11.39
SD Ch–4		**51.2**	34.02	*M. bairdii*	**FMNH PM 9466**	7.48	5.08	12.45	12.59	11.49	13.87	11.99	14.09	12.58	13.85	12.76	14.42		
SD Ch–4		36.6	34.80	*M. grandis*	**SDSM 76097**	9.35	6.14	13.56	13.21	13.90	14.60	14.19	14.99	15.05	15.54	14.01	15.56	13.44	12.30
SD Ch–4		36.6	34.80	*M. grandis*	SDSM 76161							15.67		15.51	17.36	15.89	18.02	13.64	15.51
SD Ch–4		36.6	34.80	*M. grandis*	**SDSM HW 8315**			13.65	13.44	13.83	15.09	14.22	15.13	13.81	15.48	13.84	16.04	13.92	15.05
NE Ch–3	DW-13	**-27.1**	35.64	*M. grandis*	**UNSM 131719**					15.67	15.81	15.72	15.98	15.13	15.63	15.54	15.92	14.46	14.80
SD Ch–3		**34.6**	34.95	*M. bairdii*	FMNH G 6584			13.43	12.27	12.88	14.18	12.97	14.36	13.97	13.86	12.80	14.31		
SD Ch–3		**35.6**	34.87	*M. bairdii*	FMNH PM 26250			13.14	13.29	12.63	14.97	13.81	15.36	12.96	15.30	12.66	15.29	12.30	13.88
SD Ch–3		**30.5**	35.25	*M. bairdii*	**FMNH PM 56488**			12.82	12.60	11.76	13.98	12.90	14.35	12.08	14.10	12.16	14.12	11.91	13.36
NE Ch			35.80	*M. celer*	YPM 11302							10.39	13.06	10.43	12.63		12.58	9.58	10.49
TX Ch–1			36.95	*M. celer*	FMNH PM 121	6.03	3.98	10.10	9.61	9.98	11.39	10.05	11.58	9.63	11.03	9.38	11.18		

Biozone	Locality	Strat Level	Age	Species	Specimen #	P2–4 L	M1–3 L	P2–M3 L
OR Ar-1				*M. acutidens*	**UCMP 376**	39.55	38.58	76.68
NE Wh–2	SX-15	91.1	31.50	*M. sp.*	**UNSM 131709**	35.09	36.32	70.21
SD Wh–2		187.8	30.81	*M. intermedius*	**AMNH 1196**	44.53	42.25	84.87
NE Or–4	SX-26	31.0	33.12	*M. bairdii*	UNSM 131632	33.67	32.79	65.25
NE Or–4	SX-17	30.5	33.14	*M. bairdii*	**UNSM 131633**		33.01	
NE Or–4	SX-4	34.1	33.04	*M. bairdii*	**UNSM 131667**	35.09	33.88	67.90
NE Or–4	SX-3	32.4	33.09	*M. bairdii*	**UNSM 131692**	33.88	31.80	63.92
NE Or–4		34.8	33.02	*M. bairdii*	**UNSM 131714**	35.99	34.16	66.78
NE Or–4	SX-?	31.4	33.11	*M. barbouri*	UNSM 131699	35.52		
NE Or–3	SX-39	21.7	33.37	*M. bairdii*	**UNSM 131538**	35.64	33.20	66.62
NE Or–3	SX-37	19.5	33.43	*M. bairdii*	**UNSM 131540**	36.12	34.87	68.53
NE Or–3	SX-4	26.7	33.24	*M. bairdii*	**UNSM 131543**	36.31	34.91	69.06
NE Or–3	SX-26	21.4	33.38	*M. bairdii*	**UNSM 131546**	34.86	34.14	67.94
NE Or–3	SX-26	15.3	33.55	*M. bairdii*	**UNSM 131598**	34.94	33.86	66.36
NE Or–3	SX-6	18.0	33.47	*M. bairdii*	UNSM 131602	31.69		
NE Or–3	SX-4a	17.1	33.49	*M. bairdii*	**UNSM 131615**	34.44	33.62	65.25
NE Or–3	SX-6	13.8	33.59	*M. bairdii*	**UNSM 131619**	34.68	32.87	66.42
NE Or–3	SX-6	**14.0**	33.58	*M. bairdii*	UNSM 131631		33.10	
NE Or–3	DW-?	24.5	33.30	*M. bairdii*	UNSM 131634	34.20		
NE Or–3	SX-19	22.0	33.37	*M. bairdii*	**UNSM 131668**	35.59	34.49	68.26
NE Or–3	SX-6	24.5	33.30	*M. bairdii*	UNSM 131679	36.02	35.49	
NE Or–3	DW-104	25.0	33.29	*M. barbouri*	UNSM 131515	37.64	38.03	74.53
NE Or–3	SX-26	15.6	33.54	*M. barbouri*	UNSM 131534	36.71	36.85	69.46
NE Or–3	SX-26	15.6	33.54	*M. barbouri*	UNSM 131535	35.17	37.24	70.03
NE Or–3	SX-12	24.9	33.29	*M. barbouri*	UNSM 131688	37.15	35.07	68.78
NE Or–3	SX-12	**24.1**	33.31	*M. barbouri*	UNSM 131704	36.74	35.30	69.67
NE Or–3	SX-37	16.5	33.52	*M. barbouri*	UNSM 131722		34.03	
NE Or–2	SX-24	11.6	33.65	*M. bairdii*	UNSM 131601	34.70	32.92	66.80
NE Or–2	SX-19	11.9	33.64	*M. barbouri*	UNSM 131539	37.99		
NE Or–2	SX-11	11.9	33.64	*M. barbouri*	UNSM 131545	37.84		
NE Or–1	SX-17	**5.0**	33.96	*M. bairdii*	**UNSM 131530**	33.62	33.30	66.32
NE Or–1	SX-40	2.1	34.11	*M. bairdii*	UNSM 131541	38.05	35.36	71.04
NE Or–1	SX-11/12	**5.0**	33.96	*M. bairdii*	UNSM 131551	34.64		
NE Or–1	SX-25	5.5	33.93	*M. bairdii*	**UNSM 131571**	35.30	33.13	67.57
NE Or–1	SX-26	**3.1**	34.06	*M. bairdii*	UNSM 131572	35.12		
NE Or–1	SX-25	**5.0**	33.96	*M. bairdii*	UNSM 131573	33.83	31.65	63.74
NE Or–1	Sx-18	**5.0**	33.96	*M. bairdii*	UNSM 131574	35.91		
NE Or–1	SX-11	**5.0**	33.96	*M. bairdii*	UNSM 131578	31.19		
NE Or–1	SX-12	7.0	33.85	*M. bairdii*	**UNSM 131580**	33.12	32.45	63.87
NE Or–1	SX-18	**5.0**	33.96	*M. bairdii*	UNSM 131659		34.57	

Biozone	Locality	Strat Level	Age	Species	Specimen #	P2–4 L	M1–3 L	P2–M3 L
NE Ch–4	SX-39	-2.4	34.35	*M. bairdii*	UNSM 131510		36.66	
NE Ch–4	DW-104	-1.5	34.30	*M. bairdii*	UNSM 131529	35.37	34.24	67.69
NE Ch–4	SX-18	0.0	34.22	*M. bairdii*	UNSM 131577	35.19		
NE Ch–4	Loc. 32	0.0	34.22	*M. bairdii*	**UNSM 131684**	34.64	33.15	65.72
NE Ch–4		**-6.1**	34.54	*M. bairdii*	UNSM 131721	33.05	33.36	64.35
NE Ch–4		-6.4	34.56	*M. bairdii*	UNSM 48485	35.07		
NE Ch–4	SX-18	0.0	34.22	*M. grandis*	**UNSM 131514**	41.03		
NE Ch–4	SX-0	-0.3	34.24	*M. grandis*	**UNSM 131517**	39.29		
NE Ch–3	DW-13	**-27.1**	35.64	*M. grandis*	**UNSM 131719**		40.63	

APPENDIX B

LOWER CHEEK TOOTH MEASUREMENTS

All tooth measurements in Appendix B are in millimeters (mm). Stratigraphic level is reported in meters (m), and refers to FIGURE XX. For specimens from Nebraska 0 m is the UPW, as in Zanazzi et al. (2009). In South Dakota 0 m is the base of the Ahearn Member of the Chadron Formation. Stratigraphic levels in bold indicates that the specimen is from a stratigraphic range and the average value is reported. Specimen numbers in bold indicates that both the left and right tooth rows of an individual were measured and the average value of all tooth measurements is reported. Abbreviations follow Appendix A.

TABLE B1

Biozone	Locality	Strat Level	Age	Species	Specimen #	P1L	P1W	P2L	P2W	P3L	P3W	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W
NE Wh–2	SX-15	91.1	31.40	*M. sp.*	UNSM 131709							11.57	10.37	11.19	8.87	10.57		15.66	6.97
NE Wh–2	SX-27	91.1	31.40	*M. sp.*	UNSM 131791													15.39	6.73
SD Wh–2		**187.8**	30.81	*M. sp.*	FMNH P 12546			13.22		12.28	11.45	12.73	12.23	11.43		12.52	9.60	17.51	9.40
SD Wh–2		**187.8**	30.81	*M. sp.*	FMNH P 12547					13.37	11.76	13.93	11.80	15.61	11.59	15.74	9.97	21.35	8.69
SD Wh–2		**187.8**	30.81	*M. sp.*	FMNH PM 500			13.81	10.55	14.17	12.50	14.56	12.70	13.57	10.93	14.49	10.00		
SD Wh–2		**187.8**	30.81	*M. sp.*	SDSM 2832			16.04	10.05	14.96	12.45	15.01	12.44	14.21	10.70	14.84	10.05	18.91	9.08
SD Wh–2	V401	**187.8**	30.81	*M. sp.*	**SDSM 2972**			14.30	8.76	15.05	10.84	14.49	11.61	14.26	9.98	14.20	9.51	19.80	8.26
SD Wh–2	V401	**187.8**	30.81	*M. sp.*	SDSM 40130			14.94	10.06	14.44	11.80	14.65	11.92	13.35	10.00	13.76	9.40	17.89	8.27
SD Wh–2	V401	**187.8**	30.81	*M. sp.*	SDSM 40191			11.97	8.73	11.78	9.73	11.80	10.01	11.79	8.33	11.99	7.65	15.40	7.40
SD Wh–2	V401	**187.8**	30.81	*M. sp.*	SDSM 4032			12.73	9.17	12.69	11.00	13.05	10.99	12.60	9.54	14.35	9.78	17.22	8.05
SD Wh–2	V401	**187.8**	30.81	*M. sp.*	**SDSM 4037**									16.65	11.58	16.94	11.31		
SD Wh–2	V401	**187.8**	30.81	*M. sp.*	SDSM 4041					13.39	12.14	14.10	13.36	12.53	10.60	13.96	10.13	19.38	8.85
SD Wh–2	V401	**187.8**	30.81	*M. sp.*	**SDSM 4044**					13.40	11.13	13.26	11.61	13.49	10.66	13.54	9.56	18.56	8.66
SD Wh–2	V401	**187.8**	30.81	*M. sp.*	**SDSM 4052**			14.40	10.89	14.57	12.61	15.15	13.06	15.82	10.85	14.58	9.61	19.38	8.66
SD Wh–2	V401	**187.8**	30.81	*M. sp.*	**SDSM 4080**					14.43	10.92	14.03	11.18	13.99	10.08	14.26	9.20		
SD Wh–2	V712	209.1	30.40	*M. sp.*	**SDSM 58294**	6.73	4.25	14.11	8.74	13.14	9.52	14.06	9.14	13.90	9.91	14.35	9.34		
SD Wh–2	V6810	**187.8**	30.81	*M. sp.*	SDSM 6820			15.96	10.22	13.73	11.65	15.26	12.41	14.00	11.12	14.72	9.55	17.23	8.17
SD Wh–2	V6913	**187.8**	30.81	*M. sp.*	SDSM 71795											13.44	7.58	16.99	7.10
SD Wh–2	V6917	**172.8**	31.10	*M. sp.*	**SDSM 71859**			14.21	10.16	13.88	11.24					13.89	10.29	19.06	8.07
NE Wh–1	SX-?	**40.5**	32.10	*M. sp.*	UNSM 131649											11.61	8.72	16.71	7.54
NE Wh–1	SX-43	44.4	32.00	*M. sp.*	**UNSM 131678**			13.12	8.64	12.71	10.28	13.31	10.75	13.04	9.29	12.41	8.79	16.29	7.35
NE Wh–1	SX-21	67.6	31.80	*M. sp.*	UNSM 131785													15.12	6.93
NE Wh–1	SX-23/24	48.1	32.00	*M. sp.*	**UNSM 131786**													16.07	7.15
NE Wh–1	SX-21	54.5	31.90	*M. sp.*	UNSM 131787													16.58	7.00
NE Wh–1	SX-21	66.4	31.80	*M. sp.*	UNSM 131788													16.08	7.85
NE Or–4	SX-6	**34.5**	33.03	*M. bairdii*	UNSM 131648													14.54	6.91
NE Or–4	SX-17	36.4	32.98	*M. bairdii*	UNSM 131651									10.50	8.20	10.83	7.40	14.66	6.32
NE Or–4	SX-?	35.9	32.99	*M. bairdii*	UNSM 131652													13.02	5.86
NE Or–4	SX-4	34.1	33.04	*M. bairdii*	**UNSM 131667**			10.94		11.57	9.83	11.28		10.25		10.85		14.98	
NE Or–4	SX-3	32.4	33.09	*M. bairdii*	**UNSM 131692**	3.79	2.75	11.03	7.67	10.43	9.50	11.71	9.78	10.93	8.46	10.63	7.58	14.18	6.44
NE Or–4		34.8	33.02	*M. bairdii*	**UNSM 131714**			11.30	7.65			10.86	9.68			11.38	7.75	15.18	6.85
NE Or–4	SX-17	34.9	33.02	*M. bairdii*	UNSM 131760													15.35	6.53
NE Or–4	SX-10	34.0	33.04	*M. barbouri*	UNSM 131673					12.70	9.88	12.50	10.67	12.92	8.87	12.90	8.30	16.82	7.21
NE Or–4	SX-14	37.0	32.96	*M. barbouri*	UNSM 131702			12.04	8.94	12.44	8.95	12.49	9.24	12.68	8.25			15.90	6.53
NE Or–4	SX-14	37.0	32.96	*M. barbouri*	UNSM 131777													16.05	6.50
SD Or–4		**103.1**	32.15	*M. bairdii*	FMNH PM 44705													13.42	6.43
SD Or–4	V2000-89	120.0	32.10	*M. barbouri*	SDSM 60335			11.78	8.24	12.26	10.02			13.02	8.97	12.03	7.96	16.15	7.22

Biozone	Locality	Strat Level	Age	Species	Specimen #	P1L	P1W	P2L	P2W	P3L	P3W	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W
NE Or–3	DW-104	27.4	33.22	*M. bairdii*	**UNSM 131516**	2.92	2.99	11.16	8.15	11.83	9.50	12.00	10.21	11.00	8.62	11.87	8.65	14.79	7.55
NE Or–3	SX-39	21.7	33.37	*M. bairdii*	UNSM 131538			10.62	7.31	10.80	9.33	11.02	10.34	10.39	8.27	11.48	8.07	14.72	6.51
NE Or–3	SX-4	16.5	33.52	*M. bairdii*	UNSM 131603					11.54	9.53	11.22	9.92	10.48	8.73	10.90	8.00		
NE Or–3	SX-17	28.3	33.20	*M. bairdii*	UNSM 131604							11.04	8.80	10.40	8.07	10.96	7.34		
NE Or–3	SX-24	15.9	33.53	*M. bairdii*	**UNSM 131614**			10.44	7.37	11.54	9.71	12.08	10.19	10.52	8.17	11.64	8.38	14.96	7.15
NE Or–3	SX-6	27.7	33.21	*M. bairdii*	**UNSM 131625**	3.12	2.44	10.76	6.68	11.58	8.13	11.33	8.81	10.96	8.22	11.37	7.45	14.90	
NE Or–3	SX-?	**14.0**	33.58	*M. bairdii*	UNSM 131626					10.88	9.46	11.35	9.80	10.55	8.30	10.80	7.80		
NE Or–3	SX-6	**15.3**	33.55	*M. bairdii*	UNSM 131628					10.21	9.42	9.92	9.97	9.89	8.49	10.58	7.80	13.49	6.45
NE Or–3	SX-25	**24.5**	33.30	*M. bairdii*	UNSM 131639											12.65	8.92	16.59	7.23
NE Or–3	SX-5	23.2	33.33	*M. bairdii*	UNSM 131643			10.98	7.31	11.96	8.95	11.23	8.97	11.08	7.59	12.30	8.05		
NE Or–3	SX-16	17.5	33.49	*M. bairdii*	UNSM 131646														
NE Or–3	SX-5	17.0	33.50	*M. bairdii*	UNSM 131647													14.90	7.26
NE Or–3	SX-6	24.5	33.30	*M. bairdii*	UNSM 131672													14.55	6.58
NE Or–3	SX-6	24.5	33.30	*M. bairdii*	UNSM 131679			12.66		11.72		11.26		11.27		11.47		15.98	
NE Or–3	SX-8	23.8	33.32	*M. bairdii*	UNSM 131681					11.87	8.77	11.89	9.26	10.83	8.08	11.80	7.42		
NE Or–3	SX-5	**25.5**	33.27	*M. bairdii*	**UNSM 131686**			10.45	6.82	10.63	8.76	10.82	9.38	10.55	8.50	10.96	7.73	14.44	6.71
NE Or–3	SX-4	21.4	33.38	*M. bairdii*	**UNSM 131693**	3.80	2.66	11.02	7.34	10.94	9.09	10.82	9.68	10.83		10.87	7.18	15.09	6.45
NE Or–3	SX-37	25.7	33.27	*M. bairdii*	UNSM 131703													14.06	6.57
NE Or–3	SX-6	15.8	33.53	*M. bairdii*	UNSM 131756													14.35	
NE Or–3	SX-6	**24.5**	33.30	*M. bairdii*	UNSM 131778													14.26	6.51
NE Or–3	SX-17	23.9	33.31	*M. bairdii*	UNSM 131780													14.59	6.50
NE Or–3	SX-37	19.5	33.43	*M. bairdii*	UNSM 48464					12.45	9.06	11.49	9.50	11.77	8.40	11.92	7.35	14.54	6.53
NE OR–3	SX-26	15.6	33.54	*M. barbouri*	**UNSM 131534**			10.24	7.15	11.77	8.16	12.21	8.89	11.57	7.71	12.37	7.60		
NE OR–3	SX-4	20.2	33.42	*M. barbouri*	UNSM 131613			9.98	7.47	11.74	8.95	12.00	9.57	12.25	8.24	11.89	7.91	16.20	6.68
NE OR–3	SX-6	**23.2**	33.33	*M. barbouri*	UNSM 131622											12.24	7.57	16.14	6.71
NE OR–3	SX-4	20.2	33.42	*M. barbouri*	**UNSM 131641**			15.66	9.40	14.58	11.26	14.63	11.60	15.05	10.38	15.63	9.50		
NE OR–3	SX-4	20.2	33.42	*M. barbouri*	UNSM 131645					10.65	8.91	11.38	9.44	11.60	8.34	11.98	7.93	16.19	6.74
NE OR–3	SX-38?	**14.0**	33.58	*M. barbouri*	**UNSM 131664**					11.59		11.93	9.79	12.13	8.92	11.81	8.16	15.72	7.49
NE OR–3	SX-6	24.5	33.30	*M. barbouri*	UNSM 131671					12.01	10.24	12.73		11.20				16.44	7.85
NE OR–3	SX-40	16.1	33.37	*M. barbouri*	UNSM 131680									11.97		12.39	9.01	16.12	7.03
NE OR–3	SX-12	24.9	33.29	*M. barbouri*	**UNSM 131688**	3.39	2.36	11.46	8.48	12.19	10.60	12.15	10.99	12.06	8.99	12.27	8.23		
NE OR–3	SX-4	**17.1**	33.50	*M. barbouri*	UNSM 131707					10.68	9.23	11.18	9.70	10.22		11.06	7.70	16.25	6.64
NE OR–3	SX-26	**14.0**	33.58	*M. barbouri*	UNSM 131712			10.38	7.02	10.75		11.60	9.23	10.65	8.00	11.58	7.69	15.80	6.56
SD Or–3	V6026	73.8	32.98	*M. bairdii*	**SDSM 65151**					11.77	8.75	11.43	9.28	11.33	8.16	11.48	7.61	14.72	6.68
SD Or–3	V2001-06	**78.2**	32.85	*M. bairdii*	**SDSM 69735**			9.35	6.54	10.51	7.99	10.22	8.20	11.17	7.26	11.48	7.19	13.61	7.54
SD Or–3	V807	**78.2**	32.85	*M. bairdii*	SDSM 73560			10.11	7.01	9.93	8.88	9.98	9.69	9.87		10.76	7.02	15.30	6.43
NE Or–2	SX-8	**12.7**	33.62	*M. bairdii*	**UNSM 131585**							12.02	10.02	11.39	8.55	12.14	7.97	15.22	6.48

Biozone	Locality	Strat Level	Age	Species	Specimen #	P1L	P1W	P2L	P2W	P3L	P3W	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W
NE Or–2	SX-24	11.5	33.65	*M. bairdii*	UNSM 131644													14.62	7.00
NE Or–2	SX-38	11.0	33.66	*M. bairdii*	UNSM 131690	3.96	3.24	11.87	8.60	11.47	9.59	12.28	10.07	11.65	8.64	11.26	8.33	14.91	7.39
NE Or–2	SX-19	12.6	33.62	*M. bairdii*	UNSM 131752													14.59	6.53
NE Or–2	SX-?	8.0	33.70	*M. barbouri*	UNSM 131583									12.27	9.26	13.12	8.04	16.52	7.16
NE Or–2	SX-17	12.8	33.61	*M. barbouri*	**UNSM 131597**			11.58	8.22	11.12	9.62	11.58	9.97	11.67	8.41	11.88	7.86		
NE Or–2	SX-24	9.5	33.70	*M. barbouri*	UNSM 131644					12.56	9.81	12.10	9.99	12.15	8.84	11.97	8.18	14.62	7.00
SD Or–2		**56.0**	33.48	*M. bairdii*	**FMNH P 12025**			10.18	6.90	9.84	9.04	10.17	9.45	9.42	7.83	10.24	7.54	14.43	6.80
SD Or–2		**56.0**	33.48	*M. bairdii*	FMNH P 12855					10.89	8.22	11.06	8.46	10.25	7.67	11.04	7.01	12.59	5.79
SD Or–2		**56.0**	33.48	*M. bairdii*	**FMNH PM 14417**			10.24	7.41	10.52	9.21	11.42	10.09	10.03	8.84	10.30	8.18	14.69	6.98
SD Or–2		**56.0**	33.48	*M. bairdii*	FMNH PM 43244											11.20	7.56	13.96	6.60
SD Or–2		**56.0**	33.48	*M. bairdii*	FMNH PM 43283	4.24	3.06	10.22	7.18			10.51	9.82	10.35		10.67	7.65	14.66	
SD Or–2		59.3	33.38	*M. bairdii*	FMNH PM 55668			10.85	7.24	10.87	8.60	11.38	8.91	10.89	8.15	11.04	7.45	14.71	6.81
SD Or–2		**56.0**	33.48	*M. bairdii*	FMNH PM 9217					10.38	8.31	10.14	8.39	10.55	7.48	9.78	7.11	13.54	6.02
SD Or–2		**56.0**	33.48	*M. bairdii*	FMNH PM 9856					11.02	8.28	10.52	8.54			10.95	7.20	13.51	6.20
SD Or–2		**56.0**	33.48	*M. bairdii*	FMNH PM 9903					11.11	7.72	10.64	8.22	10.82	6.40	10.63	6.58	13.55	6.04
SD Or–2	V9626	**56.0**	33.48	*M. bairdii*	**SDSM 39931**					11.21	9.05	11.47	9.84			11.57	7.56	13.90	5.91
SD Or–2	V242	**56.0**	33.48	*M. bairdii*	SDSM 424			12.53		12.25		11.95		10.99		10.85		13.86	
SD Or–2	V9626	**56.0**	33.48	*M. bairdii*	SDSM 48757			11.23	7.26	11.59	8.89			11.12	7.98	11.58	7.67	14.24	6.87
SD Or–2	V6105	**56.0**	33.48	*M. bairdii*	**SDSM 5080**			12.07	8.47	11.06	9.30	11.26	9.26	10.99	8.34	10.75	7.89	14.65	6.59
SD Or–2	V6105	**56.0**	33.48	*M. bairdii*	**SDSM 5811**			11.09	7.15	10.86	8.36	11.20	8.49	10.47	7.62	11.26	7.14	13.47	6.40
SD Or–2	V6026	**56.0**	33.48	*M. bairdii*	SDSM 59149							11.54	9.47	11.82		12.27	7.80	15.33	6.70
SD Or–2	V6026	**56.0**	33.48	*M. bairdii*	SDSM 59153			11.64		11.23		10.49		9.74		10.62			
SD Or–2	V6026	**56.0**	33.48	*M. bairdii*	SDSM 60133					11.27	8.64	10.65	9.16	10.58	7.48	10.73	7.16	13.59	6.21
SD Or–2	V6104	**56.0**	33.48	*M. bairdii*	**SDSM 6138**			10.25	7.37	10.03	8.72	10.50	9.01	10.72	7.87	10.65	6.88	13.52	6.36
SD Or–2	V6104	**56.0**	33.48	*M. bairdii*	**SDSM 6146**			10.31	6.94	10.02	8.71	10.48	9.20	9.70	7.65	10.16	7.16	13.26	6.89
SD Or–2	V6104	**56.0**	33.48	*M. bairdii*	SDSM 6153			11.58	7.36	11.21	8.82	11.82	9.15			11.16	6.98	13.58	6.39
SD Or–2	V273	60.1	33.36	*M. bairdii*	**SDSM 65150**			11.59		11.12	9.03	11.32	9.12	10.22	7.97	11.44	7.56	14.29	6.79
SD Or–2		**56.0**	33.48	*M. barbouri*	FMNH PM 43807							11.42		11.06	8.38	11.55	7.79	16.69	7.07
SD Or–2		**56.0**	33.48	*M. barbouri*	FMNH PM 9858					10.61	8.55	10.50	8.78	10.65	7.61	10.68	6.71	13.29	5.83
SD Or–2	V242	**56.0**	33.48	*M. barbouri*	**SDSM 2920**	3.52	2.75	9.80	6.92	10.18	8.13	10.47	8.79	10.36	7.69	10.20	7.14	15.40	6.67
SD Or–2		**56.0**	33.48	*M. barbouri*	**SDSM 3067**									12.39	8.05	11.18	7.15		
SD Or–2	V9626	**56.0**	33.48	*M. barbouri*	**SDSM 42739**	2.86	2.46	11.07	7.75	10.99	9.21	11.36	9.72	10.96	8.50	10.43	8.35	14.64	6.94
SD Or–2	V6105	**56.0**	33.48	*M. barbouri*	SDSM 61135									11.76	8.81	13.05	8.67	17.37	7.48
SD Or–2	V6105	**56.0**	33.48	*M. barbouri*	**SDSM 6172**			11.31	8.12	12.13	9.07	12.42	9.04	13.12	8.73	12.97	8.45	16.25	7.17
NE Or–1	SX-17	**5.0**	33.96	*M. bairdii*	**UNSM 131530**					11.14	9.51	11.63	9.72	11.78	8.49	11.63	8.04	14.82	7.11
NE Or–1	SX-26	**5.0**	33.96	*M. bairdii*	UNSM 131548			11.33	7.05	11.06	8.59	11.82	8.98	11.50	7.96	11.52	7.33		
NE Or–1	SX-26	**5.0**	33.96	*M. bairdii*	UNSM 131549									11.11	8.51	11.55	7.99	15.61	7.33

Biozone	Locality	Strat Level	Age	Species	Specimen #	P1L	P1W	P2L	P2W	P3L	P3W	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W
NE Or–1	SX-5	**5.0**	33.96	*M. bairdii*	UNSM 131557			10.34	7.10	10.88		11.05	9.59	11.25	7.97	10.80	7.67	14.98	7.11
NE Or–1	SX-25	3.9	34.02	*M. bairdii*	**UNSM 131562**	3.74	2.77	11.06	7.63	11.12	9.58	11.48	9.91	11.21	8.06	11.15	7.55	14.87	6.96
NE Or–1	SX-25	5.4	33.94	*M. bairdii*	UNSM 131571					11.20	9.45	11.02	9.54	10.96	8.57			15.08	7.07
NE Or–1	SX-26	**3.0**	34.06	*M. bairdii*	UNSM 131572					11.46	9.01	11.80	9.39	10.89	8.04	11.59	7.81		
NE Or–1	SX-11	**5.0**	33.96	*M. bairdii*	**UNSM 131578**							10.15	8.69	9.60	7.68	10.17	7.08	14.45	6.32
NE Or–1	SX-8	**5.0**	33.96	*M. bairdii*	UNSM 131581			11.10	7.55	11.22	9.17	11.18	9.58	11.16	8.33				
NE Or–1	SX-9	**5.0**	33.96	*M. bairdii*	UNSM 131586			10.92	8.00	11.71	9.80	11.80	10.35	10.96	8.84	11.97	8.16		
NE Or–1	SX-32	**5.0**	33.96	*M. bairdii*	UNSM 131587					11.95	9.11	11.30	9.62	11.11	8.12	11.01	7.31		
NE Or–1	SX-25	**5.0**	33.96	*M. bairdii*	**UNSM 131591**			9.96	7.12	10.59	8.90	10.69	9.48	10.76	8.09	11.43	7.43	14.99	6.71
NE Or–1	SX-17	**5.0**	33.96	*M. bairdii*	**UNSM 131592**					11.00	8.78	10.50	8.90	10.02	7.69	11.05	7.27	15.76	7.19
NE Or–1	SX-26	3.0	34.06	*M. bairdii*	UNSM 131593			10.89	7.96	11.13	9.57	11.58	10.16	10.98	8.41	11.90	8.24		
NE Or–1	SX-11	**5.2**	33.95	*M. bairdii*	UNSM 131595							11.80		11.18	8.11	11.54	7.71	15.17	7.27
NE Or–1	SX-26	6.1	33.90	*M. bairdii*	UNSM 131607					11.76	8.39	11.63	8.85	10.30	7.70	11.14	6.97	14.19	6.57
NE Or–1	SX-21	2.0	33.90	*M. bairdii*	**UNSM 131655**			10.66	7.91	11.00	8.82	10.77	9.18	10.90	8.28	11.57	7.64	14.72	6.83
NE Or–1	SX-18	**5.0**	33.96	*M. bairdii*	UNSM 131665					10.14	8.20	10.28	8.70	10.69	7.81	10.51	7.14		
NE Or–1	SX-18	**5.0**	33.96	*M. bairdii*	UNSM 131666					11.67	8.71	11.18	8.92	10.62	7.72	11.57	7.19		
NE Or–1	SX-26	6.1	33.90	*M. bairdii*	UNSM 131746													14.95	6.61
NE Or–1	SX-26	6.1	33.90	*M. bairdii*	UNSM 131747													14.61	6.80
NE Or–1	SX-13/13A	3.7	34.03	*M. bairdii*	UNSM 131769													14.83	7.14
NE Or–1	SX-14	3.9	34.02	*M. bairdii*	UNSM 131774													14.77	6.79
NE Or–1	SX-23	**5.4**	33.93	*M. grandis*	UNSM 131565					10.74	8.74	11.34	10.16	12.25	9.32			16.95	8.09
NE Or–1	SX-?	7.9	33.81	*M. grandis*	UNSM 131583													16.52	7.16
NE Or–1	SX-11	**5.2**	33.95	*M. grandis*	UNSM 131584					12.15	9.83	12.86	10.10	11.37	8.89	12.56	7.81		
NE Or–1	SX-29	3.0	34.06	*M. grandis*	UNSM 131656													16.16	6.50
NE Or–1	SX-19	**5.0**	33.96	*M. grandis*	UNSM 131734													17.27	7.40
NE Or–1	SX-18	**2.3**	34.10	*M. grandis*	UNSM 131739													16.10	6.92
NE Or–1	SX-8	1.0	34.17	*M. grandis*	UNSM 131750													17.46	7.17
NE Or–1	SX-"BB"	7.9	33.81	*M. grandis*	UNSM 131779													18.69	8.80
NE Ch–4	DW-104	-2.4	34.35	*M. bairdii*	UNSM 131502					12.20	9.00	11.17	9.35	10.29	7.95	11.07	7.59	14.86	6.73
NE Ch–4	SX-25	0.0	34.22	*M. bairdii*	**UNSM 131513**			10.11	5.89	11.94	9.12	11.88	9.45	11.76	8.33	11.57	8.05	15.65	6.87
NE Ch–4	Sx-26	0.0	34.22	*M. bairdii*	**UNSM 131519**			10.82	8.00	11.81	9.33	11.60	9.73	11.53	8.24	12.15	7.88	15.24	7.72
NE Ch–4	DW-104	-1.5	34.30	*M. bairdii*	**UNSM 131529**			11.22	7.82	11.87	9.26	11.74	9.45	10.86	8.20	11.10	7.60	15.43	7.26
NE Ch–4	SX-40	1.4	34.15	*M. bairdii*	UNSM 131541	3.05	2.28	12.02	7.90	11.96	9.39	11.78	10.12	11.13	8.51	11.75	8.16	15.64	7.08
NE Ch–4	SX-18	-0.5	34.24	*M. bairdii*	UNSM 131568							11.14	10.26	10.48	8.71	11.50	7.78		
NE Ch–4	SX-25	**-4.6**	34.46	*M. bairdii*	UNSM 131588							10.99	9.31	10.72	8.31	11.39	7.65	15.64	6.83
NE Ch–4	SX-34	**-6.1**	34.54	*M. bairdii*	**UNSM 131720**			11.02	8.07	11.56	9.57	11.30	9.80	11.34	8.05	11.96	7.65	15.14	6.97
NE Ch–4	SX-25	**-6.1**	34.54	*M. bairdii*	UNSM 131725													14.83	6.51

Biozone	Locality	Strat Level	Age	Species	Specimen #	P1L	P1W	P2L	P2W	P3L	P3W	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W
NE Ch–4	SX-34	-4.6	34.46	*M. bairdii*	UNSM 131731													14.77	6.42
NE Ch–4	SX-29	**-6.1**	34.54	*M. bairdii*	UNSM 131768													14.86	7.06
NE Ch–4		-8.2	34.65	*M. grandis*	FMNH PM 49946											13.16	9.08	17.59	7.86
NE Ch–4	SX-18	0.0	34.22	*M. grandis*	UNSM 131508							11.51	8.78	11.63	8.65	12.98		17.11	7.03
NE Ch–4	SX-0	-0.3	34.24	*M. grandis*	**UNSM 131517**	5.02	3.16	12.34	8.24	12.72	10.45	13.17	10.87	12.07	9.52	12.70	9.18	17.70	7.94
NE Ch–4	SX-34	**-6.1**	34.54	*M. grandis*	UNSM 131523					13.23	10.09	12.55	10.33	12.72	9.65	13.58	8.50	17.55	7.63
NE Ch–4	SX-32	**-1.5**	34.30	*M. grandis*	UNSM 131524			13.51	7.71	12.66	8.72	13.64	8.62	13.62	8.83				
NE Ch–4	SX-33	-6.9	34.58	*M. grandis*	UNSM 131525											14.32	9.11	18.54	7.63
NE Ch–4	SX-0	0.0	34.22	*M. grandis*	**UNSM 131528**			13.44	8.89	13.70	10.02	13.74	10.97	13.27	9.32	13.19	9.44	18.62	8.75
NE Ch–4	DW-?	**-6.1**	34.54	*M. grandis*	UNSM 131544							12.06	9.97			11.97	8.00	16.63	6.92
NE Ch–4	SX-25	-1.5	34.30	*M. grandis*	UNSM 131687			11.58	8.09	12.07	10.10	12.39	10.73	12.37	8.83	13.17	8.92	16.12	
NE Ch–4	SX-29	-1.8	34.32	*M. grandis*	**UNSM 131711**			12.20	7.58	11.94	9.33	11.87	10.01	12.15		12.76	7.95	17.55	7.12
NE Ch–4	SX-8	1.0	34.17	*M. grandis*	UNSM 131750													17.46	7.17
SD Ch–4		**44.1**	34.40	*M. bairdii*	FMNH PM 20066									10.67	7.70	10.90	7.22	14.26	6.37
SD Ch–4		**44.1**	34.40	*M. bairdii*	FMNH PM 9056			10.05	7.18	10.52	8.02	10.77	8.76	10.86	7.85			13.21	6.58
SD Ch–4		**51.2**	34.02	*M. bairdii*	**FMNH PM 9466**	3.59	2.47	11.14	7.94	11.24	8.64	11.39	9.38	11.69	8.26	12.04	7.87		
SD Ch–4		**44.1**	34.40	*M. grandis*	CM 9157			13.56	8.22	13.95	10.58	14.71	11.17	14.03		14.21	9.02		
SD Ch–4		**44.1**	34.40	*M. grandis*	FMNH PM 9061			14.33	7.20	12.10	7.60	12.60	7.55	12.79	8.12				
SD Ch–4	V828A/B	36.6	34.80	*M. grandis*	**SDSM 76112**			11.50	8.55	12.77	10.06	12.55	10.16	13.53	9.23	13.54	8.27	16.99	7.44
SD Ch–4	V828A/B	36.6	34.80	*M. grandis*	SDSM 76141			12.70	8.77	12.37	9.27	13.10	9.92	12.44	8.58	13.41	8.82		
SD Ch–4	V828A/B	36.6	34.80	*M. grandis*	SDSM 76163					12.80	9.53	13.88	10.13	12.60		14.87		16.95	7.35
NE Ch–3	DW-13	**-26.0**	35.59	*M. bairdii*	UNSM 131505			9.49	6.06	9.53	7.29	10.11	7.74	10.57	6.84	10.43	6.28	13.97	5.91
NE Ch–3	SX-33	-19.1	35.22	*M. bairdii*	UNSM 131728													14.60	5.87
NE Ch–3	DW-13	**-27.1**	35.64	*M. grandis*	**UNSM 131500**			12.82	8.56	14.08	10.73	13.98	11.45	14.00	9.93	15.08	9.53		
NE Ch–3	SX-33	-18.0	35.17	*M. grandis*	UNSM 131509					12.71	8.58	12.30	9.69	12.41	8.27	12.03	7.68		
NE Ch–3	DW-0	-32.3	35.92	*M. grandis*	UNSM 131683	5.46	2.95	11.58	7.22	11.93	8.94	11.98	9.55	12.76	9.50	12.23	8.07	15.90	6.84
SD Ch–3		**30.5**	33.45	*M. bairdii*	FMNH PM 20829					10.74	8.91	10.74	9.96			10.78	7.77	16.11	7.05
SD Ch–3		**32.5**	33.30	*M. bairdii*	FMNH PM 49814					12.33	8.29	12.08	8.99	13.14	8.86	11.99	7.66		
SD Ch–3		**30.5**	33.45	*M. bairdii*	FMNH PM 9165					11.12	9.54	11.34	9.93	10.40	8.72	11.09	7.80	15.40	6.46
SD Ch–3		**28.5**	33.60	*M. bairdii*	FMNH PM 9356			10.43	7.07	11.57	8.93	11.30	9.35	11.84	7.62	11.55	6.68	14.87	6.37
NE Ch–2	SX-26	-34.3	36.02	*M. grandis*	UNSM 131542					13.34	9.22	14.02	9.90	13.81	8.64	13.70	8.28		
SD Ch–2		**20.0**	35.79	*M. bairdii*	FMNH PM 14642			10.38	6.53	10.46	9.74	11.18	10.42	10.69	9.46	11.12	8.69		
TX Ch–1			36.95	*M. celer*	FMNH PM 107			8.74	4.96	9.04	6.83	9.07	7.52	8.75	6.84	9.02	6.52	12.46	5.47
TX Ch–1			36.95	*M. celer*	FMNH PM 142											9.41	6.53	11.96	5.81
TX Ch–1			36.95	*M. celer*	FMNH PM 151											8.71	6.36	11.66	5.45

APPENDIX C

PREORBITAL FOSSA MEASUREMENTS

All preorbital fossa measurements in Appendix C are in millimeters (mm).

ABBREVIATIONS: **L**, length, **H**, height, **D**, depth.

TABLE C1

Species	Locality	Specimen #	L	H	D	Size	L/Size	H/Size	D/Size
M. intermedius		AMNH 1196	59.67	23.13	5.85	5.56	10.73	4.16	1.05
M. acutidens		UCMP 376	69.95	27.10	4.85	5.26	13.29	5.15	0.92
M. grandis	SX-18	UNSM 131514	57.96	30.98	5.47	5.53	10.48	5.60	0.99
M. bairdii	Loc. 32	UNSM 131684	52.84	19.83	4.74				
M. bairdii	SX-40	UNSM 131541	49.15	24.76	3.19	5.18	9.48	4.78	0.62
M. bairdii	SX-4a	UNSM 131615		17.89	4.08	5.16		3.47	0.79
M. bairdii	SX-19	UNSM 131668	45.03	21.05	4.40	5.16	8.73	4.08	0.85
M. bairdii	SX-4	UNSM 131667	49.17	19.28	5.45	5.07	9.71	3.81	1.08
M. bairdii	SX-4	UNSM 131543	63.27	17.28		5.12	12.35	3.37	
M. bairdii	SX-6	UNSM 131679	51.43	22.49	4.10				
M. barbouri	SX-19	UNSM 131539	49.72	17.39	4.42				
M. barbouri	DW-104	UNSM 131515	62.52	21.34	5.48	5.34	11.71	4.00	1.03
M. bairdii		UNSM 131793	49.40	20.05	3.92				

APPENDIX D

METATARSAL III MEASUREMENTS

All metatarsal measurements in Appendix D are in millimeters (mm)

ABBREVIATIONS: **L**, metatarsal III length, **P. A. L**, length of surface pre-articular facet, **P. A. W**, width of surface pre-articular facet, **A. F. L**, length of articular facet, **A. F. W**, width of articular facet, **N/A**, not applicable because articular facet not present.

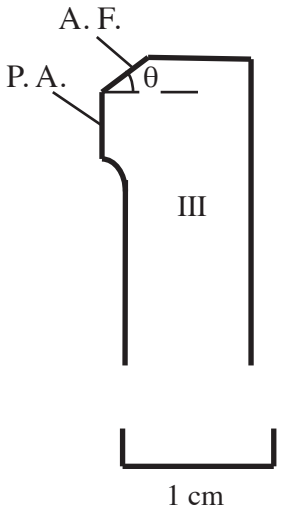

FIGURE D1. Third metatarsal of *Miohippus*, with features measured. **Abbreviations: P. A.**, pre-articular facet surface, **A. F.**, articular facet, **θ**, angle of inclination.

TABLE D1

Species	Locality	Specimen	L	P.A. L	P.A. W	Area	A. F. L	A.F. W	Area	Angle
M. grandis	SX-18	UNSM 131514	115.11	4.55	3.20	14.56	4.10	3.90	15.99	39.00
M. sp.	SX-26	UNSM 131521		2.15	2.88	6.19	2.82	3.44	9.70	54.00
M. sp.		UNSM 131533	111.91	3.96	2.92	11.56	N/A	N/A	N/A	N/A
M. sp.		UNSM 131559	111.21	3.44	3.74	12.87	1.55	3.20	4.96	51.00
M. sp.		UNSM 131560		3.55	2.47	8.77	1.46	2.42	3.53	46.00
M. sp.		UNSM 131563		4.43	3.02	13.38	N/A	N/A	N/A	N/A
M. sp.	SX-6	UNSM 131596		3.23	3.26	10.53	2.24	3.85	8.62	55.00
M. sp.	SX-26	UNSM 131609		3.82	3.07	11.73	N/A	N/A	N/A	N/A
M. sp.	SX-11/12	UNSM 131612		2.02	2.19	4.42	1.61	2.04	3.28	48.50
M. sp.	SX-19	UNSM 131618		3.09	2.35	7.26	2.62	3.29	8.62	46.00
M. sp.	SX-31	UNSM 131669		3.61	3.15	11.37	2.06	3.30	6.80	63.00
M. sp.	SX-18	UNSM 131674		3.10	3.08	9.55	N/A	N/A	N/A	N/A
M. sp.	SX-25	UNSM 131687		2.62	3.31	8.66	3.43	3.60	12.33	48.50
M. sp.	SX-11	UNSM 131710		2.77	2.96	8.20	2.00	2.83	5.66	45.00
M. sp.		UNSM 131796		3.78	3.26	12.32	N/A	N/A	N/A	N/A
M. sp.		UNSM 131797		2.92	3.16	9.21	3.49	2.85	9.91	44.25
M. sp.		UNSM 131798		3.01	2.01	6.05	1.07	1.63	1.74	50.00
M. sp.		UNSM 131799		2.03	3.06	6.21	2.16	2.46	5.31	53.50
M. sp.		UNSM 131799		3.90	3.30	12.87	N/A	N/A	N/A	N/A
M. sp.		UNSM 131800		3.59	3.16	11.34	N/A	N/A	N/A	N/A
M. sp.		UNSM 1367		3.67	2.76	10.13	N/A	N/A	N/A	N/A
M. sp.		UNSM131795		2.41	2.71	6.53	2.35	2.62	6.16	52.00